Spatio-Temporal Dynamics in Adaptive Multispecies Competitive Communities

by

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Thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Mathematics in the Faculty of Science at Stellenbosch University

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April 2019

Declaration

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Date: January 30, 2019

Abstract

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Thesis: MSc

December 2018

An ecosystem is made up of a diverse range of species interacting with each other to form complex networks though suggested being unstable contrary to the naturally observed multispecies coexistence. To solve this paradox, species interaction switching and spatial flows have been postulated as among the factors shaping community structures and stability. Historically, these studies have considered only simple community models focussing on specific forms of interaction switching with little attention to the comparison of the different switching criteria. Using May's ideology of applying random matrices theory, I attempt to understand the effect of community complexity in the presence of adaptation and species spatial flows in competitive ecosystems. Here, I use a modified Lotka-Volterra model in which species adaptively switch their interaction partner by either elimination of the unfit or survival of the fittest switching interchangeably in single communities and metacommunities. I showed that adaptive switching improves community productivity, nestedness, resilience, and diversity with increased complexity having a negative relation to productivity, resilience, and competitiveness. Species spatial movement further enhances stability and productivity. I argue that adaptive switching is an essential element of understanding the maintenance of community diversity in the presence of community complexity.

Uittreksel

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("Spatio-Temporal Dynamics in Adaptive Multispecies Competitive Communities")

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Tesis: MSc

Desember 2018

Acknowledgements

Foremost, I wish to express my sincere gratitude to my supervisor Prof Cang Hui and co-supervisor Dr. Henintsoa Onivola Minoarivelo for their time and consideration. Their guidance helped me get the best out of this thesis.

Special thanks Dr. Guillaume Latombe and Dr. Pietro Landi for the out of way assistance and constant advice throughout in this work.

I am thankful to the South African Research Chairs Initiative (SARChI) and African Institute for Mathematical Sciences (AIMS) program for funding this project.

To my great family and friends, I say thank you for your encouragement, continuous prayers. I record my gratitude to you for believing in me and for standing by me. You have always supported me and I will always be proud to have you as family. I sincerely appreciate you.

Dedications

To my parents and siblings, To Fedelma Nzuki and our daughter Nirvana.

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Chapter 1

Introduction

1.1 Introduction to the Problem

The world is rich in biodiversity. There is a diverse range of species we observe in ecosystems around the world that interact with each other in a variety of ways to form complex ecological systems. In the mid 20^{th} century, ecologists believed that these ecosystems are stable hence the naturally observed "balance of nature", but in the seventies, Robert May contradicted the early ideas that complex system might be stable. May's pioneering paper through mathematical rigour showed that complex systems are unstable [1] initiating the complexity-stability debate. Over the years, theoretical ecologists have suggested several metrics −for and against− to unravel the complexity-stability paradox.

In this work, I am focussing on competitive interactions (the presence of one species negatively affects the other species). To address these inconsistencies, I have incorporated adaptive interaction switching − in a single community and metacommunity − to a modified Lotka-Volterra model. Previous research has shown that both adaptive interaction switching and spatial flows of species play a significant role in community structure and stability hence its inclusion in my model.

I have categorised my work into two sections: (1) I incorporate species interaction switching in a single community (considering independent communities); (2) I combine species interaction switching and metacommunities. This work mainly focusses on Wallace's elimination of unfit and Darwin's survival of the fittest forms of interaction switching.

1.2 Complexity-stability debate

The question of a "balance of nature" has a long history in theoretical ecology and the stability-complexity debate has persisted for half a century. The central question in this debate is whether there is a relationship between complexity and stability. In the early fifties, ecologists believed that community complexity has a positive relationship with stability [2–4]. Odum [2] believed that there is a positive relationship between stability and number

of paths through which energy can flow up in a food web. Elton [4] had a strong proponent view of complex communities being more stable based on his logical conclusion from repeated observations of diverse terrestrial communities. Relatively constant populations densities characterised these communities compared to the simple ones which often experienced more violent fluctuations, such as insects outbreaks.

MacArthur [3] had a radical view on this question using a mathematical framework. He concluded that "stability increases as the number of links increases," i.e., more diverse communities are more stable. This framework used food webs to analyse both the species richness S (the number of species) and the trophic links (the proportion of interactions between species, also named connectance C). His concept was that if there is an overabundance in prey population in an ecosystem with many predators then the effect would be weakened and the prey effect on anyone predator would be negligible. However, in case of prey species increase in a place where one predator existed then this effect would be passed on in full to the predator. Thus stability would be enhanced by increasing either species richness (number of species) or connectance (number of interaction between them). The two parameters - species richness and connectance - are collectively termed "complexity" [1, 5, 6].

McCann [6] noted that these early observations of diverse ecosystems and MacArthur [3] framework were, however, based largely on observations and speculations. These early intuitions were challenged in the seventies by Levins [7, 8], Gardner and Ashby [9], and May [1] using numerical computation illustrating the exact opposite. May [1, 5] in his pioneering work showed mathematically using random matrix theory [10, 11] that large random systems destabilize beyond certain connectance threshold. May's based his work on a mathematical study on community matrices by performing a local stability analysis of the community matrices, and assuming that the system is at equilibrium.

In particular, he found that more diverse systems, compared to less diverse systems, will tend to sharply transition from stable to unstable behaviour as the number of species S, the connectance C, or the average community interaction strength σ increase beyond a critical value. He backed up with a mathematical stability criterion that community being almost stable at its equilibrium if, $\sigma\sqrt{SC} < \mu$, where μ is the community intraspecific interaction strength - popularly known as the May's stability criterion.

It has been more than 40 years after May's [1, 5] pioneering work and there is still no concrete agreement on the complexity-stability relationship in the ecosystems. For instance, Haydon [12] found stability increases with community strengths and Neutel et al. [13] showed how non-random community strength pattern in naturally assembled communities explain stability. Recently, Allesina and collaborators [14, 15] have also revisited May's work and have established stability criteria for systems where species interact specifically via either mutualism, competition, or predation. Other hypotheses such as adaptive foraging [16, 17], considering hybrid community structures [18, 19] and higher order interactions

[20] have been suggested to enhance an increase in community stability. These inconsistencies may be attributed to the use of different definitions and measures for both complexity and stability and the use of models versus real ecosystems data. Moreover, the adaptation and evolution of resident species have only recently started being explored, and their contribution to the debate is no doubt important. In conclusion, the complexity-stability question is still a long−standing quest for ecologists.

1.3 Motivation

Multispecies interactions in nature form complex ecological communities of coexisting species. Theoretical studies[1, 7–9] have shown that large complex communities are unstable; contrary to the naturally observed coexistence of species. This disparity in theory and observations have inspired ecologists to try to understand the influence of species interactions and their network structure on species coexistence [14, 18, 21].

To date, views on the complexity-stability question differ strongly between ecologists; some believe that complex communities must be stable [22, 23], while others maintain that complex communities are unstable [24]. Recently, Mougi and Kondoh [18, 19] suggested a hypothesis to solve this puzzle with focus on adaptation in a hybrid community.

One form of species adaptation is via switching of interactions. A species can change its interacting partner in a community in response to a shifting ecological and environmental context. Evidence for such adaptive interaction switching, or adaptive rewiring, is mounting especially in the field of adaptive foraging where species optimizes its diet for the maximum rate of energy uptake [25], and in the field of interaction fidelity and promiscuity [26]. Previous studies have shown that this adaptive behaviour is evident in antagonistic networks. [27–29]. For instance, in a predator-prey network, the predator often switches between the prey species depending on how much it benefits from the interaction with an individual prey species. On the other hand, the prey too may devise means of minimising the predator exploitation, hence forcing the predator to switch. Also, evidence has shown species often switch their interaction partners in mutualistic networks [30, 31]. For instance, in a pollination network, pollinators continually switch the plant species with which they interact in response to environmental disturbances and the availability of resources [32], whereas plants can also adjust phenology and morphology to affect their pollinators [33, 34].

Species interaction switching has been postulated as one of the factors enabling species coexistence [18] and minimising species competitive exclusion [16, 17]. Ecological theory has also shown that switching is one of the factors that shape community structure thereby altering species way of interactions [28, 30]. Murdoch [27] unravelled that switching is vital in promoting critical processes to support improved species diverseness.

In a competitive environment, I consider switching as when the competing species always prefer interactions with species over which it has a competitive advantage. Thus, switching is observed when choosing a less competitive species over a superior competitor. For instance, the American alligator and American crocodile live in different habitats to minimize competition. in addition, Carnicer and collaborators [35] empirically showed that bird switching pattern contributes to their coexistence in the presence of competition for food. Also in human communities, people often opt for new resources which are more useful and essential for their needs.

Over the years different forms of switching have been implemented in literature namely: survival through selection and switching interaction partners [28]; decision-making from profitability and encounter rate or abundance [25]; the elimination of the unfit [29, 30]; and Darwin's survival of the fittest [16, 31]. In this thesis, I shall focus on the elimination of the unfit (henceforth elimination switching) and the survival of the fittest (henceforth optimization switching). I consider an elimination switching as when a species drops a superior competitor from its group of interacting partners and randomly chooses a new species. While optimization switching is when a species maximise its interaction benefits by repeatedly rewiring its interactions to target the most beneficial one.

In addition to the numerous hypotheses suggested to solve the complexity-stability problem, recently, spatial dynamics has been proposed where species spatial flows across ecological patches can be a major influence on species diversity. Numerous theoretical [8, 36–38] and experimental [39] studies have proven that dispersal can both facilitate or destabilize species coexistence.

In this work, I aim to unravel the influence of adaptive interaction switching in a single multispecies community (considering isolated/independent patches) and expand my results to accommodate spatial dynamics. However, previous studies have focused on specific forms of switching criteria with little or no focus on comparing different forms of switching when elucidating the complexity-stability debate.

This remains an outstanding issue on how comparisons of both optimization and elimination switching influence community structure with respect to May's criteria. I attempt to draw insights on which algorithms perform better on addressing theoretical and nature inconsistencies pertaining complexity-stability debate. By incorporating either optimized or elimination switching behaviour in a modified Lotka−Volterra model, I test their influence on the population dynamics in isolated patches and connected multipatch community.

1.4 Research objectives

The primary goal of this study is to understand the influence of switching to complexity-stability paradox. To achieve this goal, I incorporate adaptive interaction switching onto a competition Lotka-Volterra model. To get a deeper understanding of the problem, I have considered the influence of switching on a single community and metacommunity. More

precisely, my objectives are:

i To incorporate elimination and optimization switching into a modified Lotka-Volterra model in simulating the competitive species dynamics in a single and metacommunity.

ii To revisit the complexity-stability paradox by checking the influence of species interaction switching with more focus on the influence of σ on interspecific competitive interaction strength, connectance C and community size S.

iii To derive a new complexity-stability measure putting into consideration the switching factor.

1.5 Thesis outline

To address the above research objectives, I have organised this thesis as follows: in chapter 2 I give an overview of ecological networks with a focus on competitive networks and models. I also look at species interaction switching. Chapter 3 covers on single community model development, simulations, the implementation of two switching algorithms, and a summary. In chapter 4 covers the broader aspect of chapter 3 where I are considering species spatial flows. In this chapter, I develop a multispecies multipatch model. I give a general conclusion in Chapter 5 with future perspectives of my work.

Chapter 2

Literature review

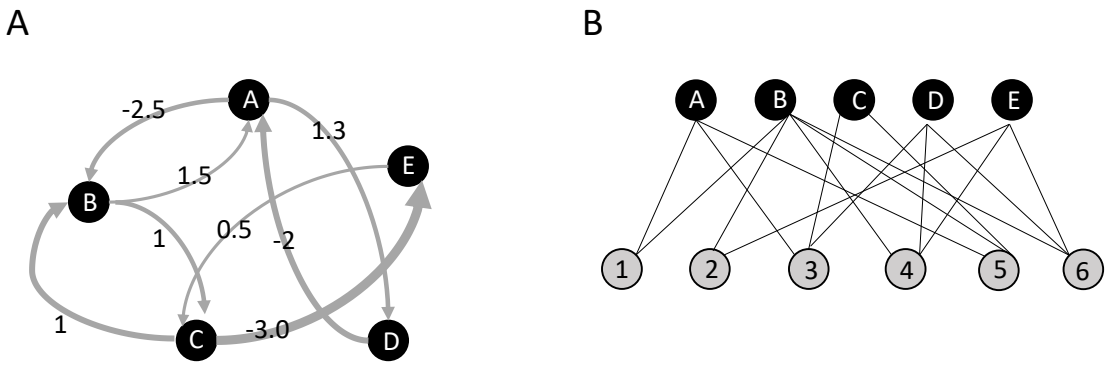
2.1 Introduction

In this chapter, I give a brief overview of the literature on dynamics of ecological networks with a special focus on competitive networks. Firstly, I introduce on ecological networks by defining the basic terminologies of a network and then the different types of ecological networks. Secondly, I shall highlight on the various descriptors of an ecological network structure and network functioning where I describe stability analysis and measure of diversity. Finally, I introduce on species interaction switching with an in-depth focus on Wallace's elimination of unfit and Darwin's survival of the fittest forms of switching.

2.2 Overview on ecological networks

Species in nature interacts with both the environment and other species forming a complex ecological network. An ecological network is a representation of biotic interactions which can used to describe real ecosystem structure. These interactions are useful for the functioning of ecosystem and survival of species.

Ecological networks can efficiently be represented using mathematical formalism of graph theory. A graph is defined as an ordered pair (V, E), where every element of the edges (E) is a two-element subset of the vertices (or nodes) (V). In perspective of ecology, data on species interactions are often a representation of different groups of edges or nodes joined together in pairs by edges forming networks. This network can be categorised according to their edge type or node group. The edge type category can either be *directed* (for instance, X eats Y, Fig. 2.1(a)), or *undirected* (for instance, X and Y compete); *weighted* (e.g. X eats Y and receives a certain amount of energy from Y) or *unweighted* (e.g. X pollinates Y). On the other hand, according to node groups are *unipartite* or *bipartite*. Unipartite networks are those in which any two nodes can be connected; for instance, social networks. On the other hand, bipartite networks have nodes that can be classified in disjoint groups such that the edge exists only between groups. For instance, parasites and hosts, plants and their insect pollinators can be represented as bipartite networks since they from two distinct groups of



	A	B	C	D	E
A	0	-2.5	0	1.3	0
B	1.5	0	1	0	0
C	0	1	0	0	-3
D	-2	0	0	0	0
E	0	0	0.5	0	0

	1	2	3	4	5	6
A	1	0	1	0	1	0
B	1	1	0	1	1	1
C	0	0	1	0	1	0
D	0	0	1	1	0	1
E	0	1	0	1	1	1

Figure 2.1: Graphical illustration of networks and their adjacency matrices. (a) A weighted directed unipartite network; (b) an unweighted undirected bipartite network. Figure redrawn from Hui et al. [40].

organisms.

These various types of species interaction can form networks of interactions that have often been visualized using interaction matrices whose elements are species interaction strengths. These matrices are known as adjacency matrices whose elements α_{kl} represents the impact of species l on species k. Consequently, the kind of biotic interaction relies upon the relative interaction strengths between the interacting species upon one another. Specifically, if $\alpha_{kl} < 0$ and $\alpha_{lk} < 0$, species k and l adversely affecting one another, this interaction is *competitive*. When species k and l have positive influence on one another (i.e., $\alpha_{kl} > 0$ and $\alpha_{lk} > 0$), it is a *mutualistic* interaction. If $\alpha_{kl} < 0$ and $\alpha_{lk} = 0$, then it is *amensalistic* interaction and If $\alpha_{kl} > 0$ and $\alpha_{lk} = 0$, the interaction is *commensalistic*. If $\alpha_{kl} > 0$ and $\alpha_{lk} < 0$, the interaction is *antagonistic*. I shall describe further on the types of ecological networks in the next section.

2.3 Types of ecological interaction networks

Mutualistic

A mutualistic interaction occurs between two or more species in which the interacting species have mutual benefit. A common example is pollination of a flowering plant by a hummingbird or an insect. In this instance, the pollinator benefits from nectar and the plant gets pollen transfer to another plant.

Antagonistic

In antagonistic interaction, one organism benefits at the expense of another. A good example is a predation in which one organism captures biomass from the other. Predation is also often referred to as carnivory but commonly known as all forms of one organism eating another, regardless of the closeness of association (i.e., parasitism), trophic level (i.e., herbivory) and harm inflicted on the prey (i.e., grazing).

Competition

Competitive interactions are those which occur when individuals negatively influence each other's population growth rates due to limited supply of a resource such as light, territory or space, food, and mates [41]. There are different types of competition namely exploitative, interference and pre-emptive competitions.

Exploitative competition: the competing species depress one another through the use of a shared resource i.e., nutrient or food. For example, tropical reef fish that graze on the same kind of algae and desert plants that compete for a limited supply of water.

Interference competition: the competing individuals or populations behave in a manner that minimizes the exploitation efficiency of another competing partner or individual. For instance, songbirds that maintain well-established breeding territories.

Preemptive competition: combination of both exploitative and interference competition where individuals monopolizes space by preventing other potential competitors from accessing shared resources.

Competition can happen among individuals of same species (intraspecific competition) or between two or more different species (interspecific competition). Fig. 2.2 shows the two distinct forms of competitive interactions.

(a)

(b)

Figure 2.2: **Competitive interactions.** 2.2a is an illustration of an interspecific competition where a lion and hyena are fighting for food in a park. 2.2b is an illustration of intraspecific competition where the bighorn sheep - known for head encounters- are fighting for females. Photo (a) by Brittany Gunther [42] and (b) by Stephen Torbit [43].

Amensalistic

This interaction occurs when one species inflicts harm on the other interacting partner without itself receiving any benefits. For instance, cattle trampling on grass. In this case, the grass causes negligible effects on the cattle hoof while the grass is being crushed. For example, **allelopathy**, where an organism produces biochemicals that influence the reproduction, survival and growth of its interacting partners. In allelopathy, due to the chemicals produced by one organism, the other interacting partner may not survive.

Commensalistic

It is an interaction between two organisms in which one benefits and the other organism is neither harmed nor benefiting. It occurs when one organism benefits by interacting with another organism by which the host is not affected. For example, an epiphyte plant (such as orchid species) grows on other plants to have better access to sunlight and moisture. These plants have specialized roots to enhance moisture and nutrients absorption from the humid air for food preparation, so they do not depend on host species.

In regards to the effect of the interactions on each of the involved species, the different types of interactions can be summarized in table 2.1.

Table 2.1: Classification of ecological interactions

Type of interaction	Effect (sign)	Effects
Mutualistic	+ /+	interaction beneficial to both species
Antagonistic	- / +	one species benefits, one is adversely affected
Competition	- / -	each species adversely affected
Amensalistic	- / 0	one species adversely affected, one unaffected
Commensalistic	+ / 0	one species benefits, one unaffected

2.4 Descriptors of complex network structure

Small networks are characterised by few nodes and edges hence a simple graphical visualization of a network can be clearly illustrated. However, large networks are complex in nature defined by numerous nodes making graphical representation incomprehensible. Nonetheless, a number of network measures have been developed specifically for this function.

Connectance

It is the number of actual possible links expressed as a proportion of the total number of possible links [44]. For a unipartite network, connectance (C) is computed as:

$$C = \frac{L}{S^2}$$

where L is the the total number of interactions and S^2 is the total number of possible interactions. whereas, in a bipartite network,

$$C = \frac{L}{n_1 + n_2}$$

where n_1 and n_2 are the numbers of species in the two distinct groups. Occasionally, *connectivity*, often used instead of connectance, is the total number of interactions (L) in a network. Connectance is an important property in fostering community stability hence being widely used as a measure of food web complexity.

Degree distribution

In graph theory, the degree of a node in a network is the number of connection of that node. In ecology, degree distribution is the distribution of the number of links per species. The distribution function $P(k)$ denotes the probability that a node selected at random has exactly k edges [45]. The plot of $P(k)$ is an histogram of the degrees of the nodes, which then represents the number of nodes that have that number of edges. Early studies on networks revealed that social networks degree distributions follow a power law [45]. However, ecological networks tend not to be scale-free. For instance, in food webs, [46] found that they follow an exponential distribution.

Clustering Coefficient

Clustering coefficient property was popularized in 1998 Nature paper by Watts and Strogatz [47].
For a given node i, with t_i neighbours, the degree of clustering around node i is defined as the proportion of links that exist between t_i neighbours and the number of maximum possible interactions between neighbours of t_i. For a given node A, the clustering coefficient

cc(A) is

$$cc(A) := \frac{\text{No. of interactions between neighbours of A}}{\text{No. of maximum interactions between neighbours of A}} \tag{2.1}$$

For a network, N

$$CC(N) = \frac{1}{\text{No. of nodes}} \sum_{\text{n}} CC(n) \tag{2.2}$$

A simple illustration is shown in Fig 2.3.

Modularity

Ecological networks are often composed of sub-communities often referred to as modules. Each module is a cluster of species, that are closely connected to one another than to species in different modules. Identifying such modules has a potential to develop a better understanding of the assembly of ecological communities.

Over the years several algorithms for quantifying the level of modularity in a network have been proposed (see [48–50]). Simulated annealing optimization approach is one of the widely used algorithm to compute modularity.

For a given network, simulated annealing algorithm is optimizing a modularity measurement M defined as:

$$M = \sum_{n=1}^{\tau} \left[\frac{l_n}{L} - \left(\frac{d_n}{2L} \right)^2 \right] \tag{2.3}$$

where τ is the number of modules, d_n is the sum of the degrees of the nodes in module n, L is the number of links in the network, and l_n is the number of links between nodes in module n. An example of a highly modular network is shown in Fig. 2.3.

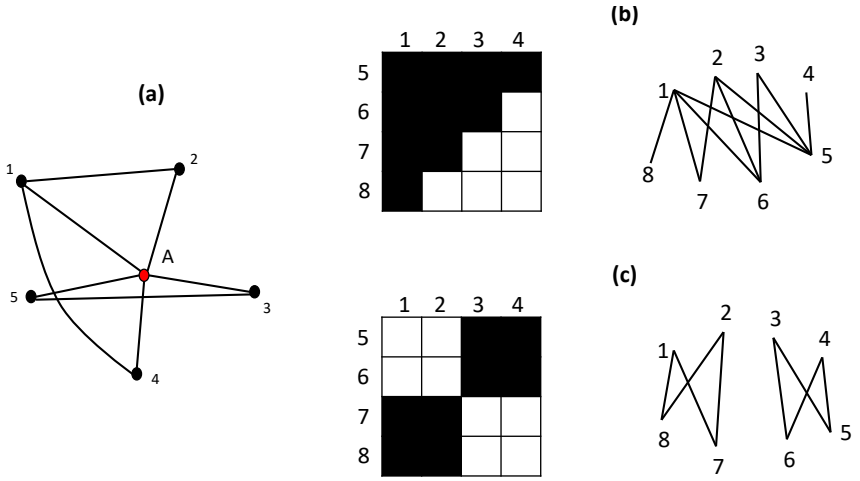


Figure 2.3: **Descriptors of network structure. (a)** clustering coefficient. Sample graph to illustrate the calculation of cc(A). Three of the A's neighbours are connected to each other ($1-2$, $1-4$, and $3-5$). Hence, there are a total of $\binom{5}{2}$ pairs of neighbours. Thus, cc(A) = $\frac{3}{\binom{5}{2}} = 0.3$. **(b)** perfect nested network. **(c)** Highly modular network.

Nestedness

Nestedness is an hierarchical pattern of interaction in which specialist species (i.e. with few interactions) can only interact with a subset of the species with which generalists (i.e. those with high number of interactions) interact. The concept of nestedness was initially introduced as a measure for species-site interaction, but over the years it gained huge popularity as metric for bipartite species networks.

Nestedness was at first computed from a presence-absence matrix where rows are species and columns are sampling sites along some environmental or spatial gradients. Various nestedness measurements have been proposed however disagree considerably in their derivations. These measures are Spectral radius (SR), Manhattan distance (MD), measure of Johnson, Dominguez-Garcia & Munoz (JDM), discrepancy (BR), nestedness temperature calculator (NTC) and nestedness based on overlap and decreasing fill (NODF). I briefly describe these measures in Table 2.2. Recently, NODF has received huge acceptance as a preferred nestedness measure hence my in-depth description.

Table 2.2: Summary of nestedness measures

Name	Initials	Description	Reference
Nestedness temperature calculator	NTC	Difference from an 'isocline of perfect order'	[51]
Spectral radius	SR	lead eigenvalue of the adjacency matrix	[52]
Discrepancy	BR	Difference from a 'maximal packed' matrix	[53]
Manhattan distance	MD	Sum of row and column indexes of connections	[54]
Johnson,Dominguez-Garcia & Munoz	JDM	Measure of dissassortivity using configuration model	[55]
Nestedness based on overlap and decreasing fill	NODF	pairwise row and column comparisons	[56]
Weighted NODF	WNODF	Weighted version of NODF	[57]

NODF was first introduced by Almeida-Neto et al. [56] and has since became a popular metric to quantify nestedness of a matrix. NODF can be computed as:

$$NODF = \frac{N_{row} + N_{col}}{\frac{r(r-1)}{2} + \frac{c(c-1)}{2}} = \frac{2\left(N_{row} + N_{col}\right)}{r(r-1) + c(c-1)} \tag{2.4}$$

Here r and c are the number of rows and columns. N_{row} is the pairwise comparison of row scores, computed by taking a sum of scores for pairwise comparison of each row against all rows below it. If both rows have equal degree, then the score is equal to zero. For those rows with different degrees, the score is a percentage of all the elements in the second row equivalent to the one in first row. Similarly, N_{col} is computed by taking the pairwise comparisons of each column against those appearing to the right. $NODF$ is then computed by normalizing the sum of N_{row} and N_{col} by the sum of paired comparisons. Values for NODF are between 0 (No nestedness) and 100 (perfect nestedness). A graphical illustration of a perfect nested network is shown in Fig 2.3.

The concept of nestedness has been instrumental in ecological communities structuring, for instance, Bastolla et al. [58] hypothesized that nested structures enhances diversity by minimizing species competition among species in a community.

2.5 Models of competitive communities

The model of competitive community community I develop in this thesis is inspired from the Lotka-Volterra model which was introduced by Alfred Lotka and Vito Volterra in the

early 1920's. This was a modification of the logistic growth equation introduced by the Belgium mathematician Verhurst which forms the basis of many ecological models [41]. Verhulst's logistic equation is:

$$\frac{dX_t}{dt} = rX_t\left(1 - \frac{X_t}{K}\right) \tag{2.5}$$

where X_t is the population size at time t , r is the per capita rate of increase and K is the maximum population size the ecosystem can support, always referred to as carrying capacity.

Using the logistic equation ideology, Alfred Lotka and Vito Volterra developed a quantitative theory of competition by introducing the so-called Lotka-Volterra equations which have greatly influenced the modern ecological theory. These equations are a 2-species competition models with their species abundances denoted X_1 and X_2. All factors held constant, these two species populations grow in a logistic manner with respective intrinsic growth rates (r_1 and r_2) to their saturation point, K_1 and K_2 respectively. The model is further affected by both intraspecific competition and interspecific competition (α_{ii} and α_{ij}).

A 2-species Lotka-Volterra equations is given as

$$\begin{aligned}\frac{dX_1}{dt} &= r_1X_1\left(1 - \frac{X_1 + \alpha_{12}X_2}{K_1}\right)\\ \frac{dX_2}{dt} &= r_2X_2\left(1 - \frac{X_2 + \alpha_{21}X_1}{K_2}\right)\end{aligned} \tag{2.6}$$

where r_1, r_2 are the intrinsic growth rates and α_{12} and α_{12} are competition coefficients. α_{12} measures the effect of species 2 on the growth of species 1. If $\alpha_{12} = 1$, the per capita intraspecific effect is equal to interspecific effect. If $\alpha_{12} < 1$, then the intraspecific effect is greater than interspecific effect i.e., a population growth of species 1 is affected more by addition of members of X_1 than by addition of members of X_2. If $\alpha_{12} > 1$, the per capita interspecific effects is greater than per capita effect of intraspecific competition. If $\alpha_{12} = 0$, there is no competition and the system reduces to a logistic equation, the species population will grow sigmoidally according to the Verhulst's logistic equation but up to their individual carrying capacity [41].

Similar arguments apply to α_{21} (competitive effect of species 2 on species 1).

2.6 Linear stability analysis

Stability can be defined as the tendency of a community to rebound from change (often conned as resilience) or defy change (resistance). Allesina and Tang [14] defined stability as the ability for a system to return to equilibrium when a small disturbance is introduced. For linear systems, linear stability analysis is used to check the stability of a steady state for

a system of linear differential equations.
Robert May pioneered stability analysis for ecological communities in the early seventies [5] through mathematical approach. This entails species abundances organized as a system of differential equations enabling stability to be tested by linearising the system at an equilibrium point.

Let

$$\frac{d}{dt}\vec{x}(t) = \dot{\vec{x}}(t) = f(\vec{x}(t)); \vec{x} \in \mathbb{R}^n$$

be a system of n ordinary differential equations (ODEs).

Suppose $\vec{x}^*$ is an equilibrium point, then $f(x^*) = 0$. Applying a multivariate Taylor expansion on the right-side of the community dynamics equation at the equilibrium point x^* I have:

$$\begin{aligned}\dot{\vec{x}} &= \underbrace{f(x^*)}_{=0} + \frac{\delta f}{\delta x}\bigg|_{x^*}(x - x^*) + \frac{\delta^2 f}{\delta x^2}\bigg|_{x^*}\frac{(x-x^*)^2}{2!} + \cdots \\ &= \frac{\delta f}{\delta x}\bigg|_{x^*}(x - x^*) + \frac{\delta^2 f}{\delta x^2}\bigg|_{x^*}\frac{(x-x^*)^2}{2!} + \cdots\end{aligned}$$

The partial derivative forms the Jacobian matrix of $f(x)$.
I now define $\vec{\delta}(x) = \vec{x} - \vec{x}^*$ a small disturbance at the fixed point. Its derivative is $\dot{\vec{\delta}}(x) = \dot{\vec{x}}$.

Since $\vec{\delta}(x)$ is small, then only the first term in the equation is significant since higher terms are powers of small disturbance at equilibrium.
Then I have

$$\dot{\vec{\delta}}(x) = J^*\vec{\delta}(x) \tag{2.7}$$

Since equation 2.7 is a system of linear differential equations, I can express the solution as a superposition of terms of the form $e^{\lambda_j t}$ where λ_j is the set of eigenvalues of the Jacobian.

The eigenvalues of the Jacobian are generally complex numbers. Let $\lambda_j t = \mu_j + iv_j$, where μ_j and v_j are the real and imaginary parts of the eigenvalue. Thus,

$$e^{\lambda_j t} = e^{\mu_j + iv_j} = e^{\mu_j}e^{iv_j} = e^{\mu_j}(cos(v_j t) + isin(v_j t))$$

The real parts matters while the complex part of the eigenvalue contributes to the oscillation.

- If $\mu_j > 0$ for any j, a small disturbance grows to infinity as $t \to \infty$, i.e., the systems moves away from equilibrium hence unstable.

- If $\mu_j < 0 \; \forall j$, a small disturbance vanishes as $t \to \infty$, i.e., the system is stable.
- if $\mu_j = 0$ but non zero imaginary parts then the system oscillates.

Another way of predicting the stability of a dynamical system characterized by a random matrix is using the Girko's circular law [59]. Let us consider a S *by* S matrix of connectance C, and of which coefficients are independently distributed from any distribution with mean 0 and standard deviation σ. Girko guarantees that:

"As the size of the matrix gets large, the eigenvalues of the matrix are uniformly distributed on a circle centred at $(0, 0)$ and of radius $(R = \sigma\sqrt{(S-1)C})$ on a complex plane. Then, if the circle is shifted at $(-\mu, 0)$, where μ is the mean of the diagonal coefficients, the radius of the circle must be less than μ for stability to take place, making all the eigenvalues to be at the left hand side of the complex plane."

Hence local stability is dependent on two components: (i) increasing the elements of the diagonals, which in the case of a matrix of competitive interactions, correspond to the strength of intraspecific competition. This implies, shifting the centre of circle to more negative values and/or (ii) reducing system complexity hence reduced circle radius (Fig. 2.4).

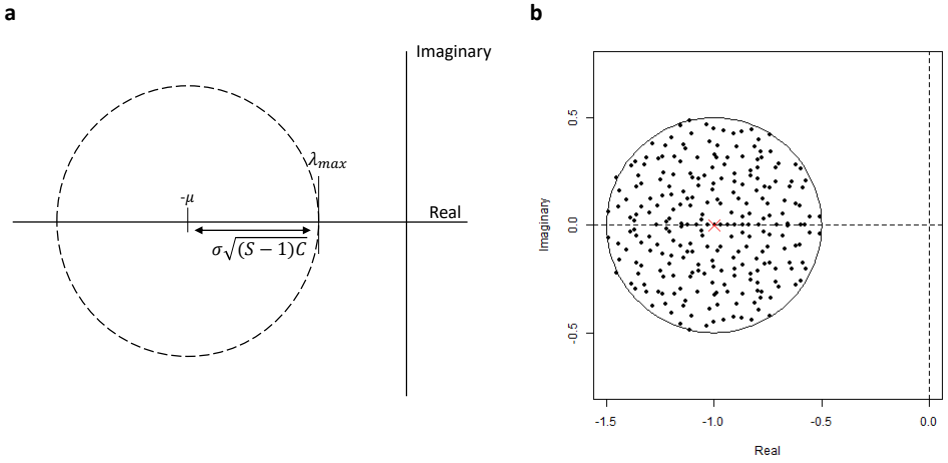


Figure 2.4: **Stability of random matrices. (a)** The eigenvalues of a large community matrix are uniformly distributed on the circle of radius $R = \sigma\sqrt{(S-1)C}$ on the complex plane. The lead eigenvalue $\text{Re}(\lambda_{max} = R - \mu)$ is on the real axis. **b.** Illustration of eigenvalues distribution of a random community matrix of $S = 250$, $C = 0.1$, $\sigma = 0$, and $\mu = 1$. The red star is the centre of the circle $(-\mu)$, the mean intraspecific strength. This is an example of a stable community $(\lambda_{max} < 0)$.

2.7 Diversity

Understanding the general patterns that underline the structure of a community is deeply rooted in understanding the community ecology. An example of such pattern is the occur-

rence of species, how some species do not occur together in the same location. Competition might be the cause of such patterns in which some species exclude others in certain locations. According to Verberk [60], understanding the species occurrence pattern is important in providing insight into the minute facets of a community and its functions. For instance, two species may occur in many locations but the two do not co-occur in larger densities (implying one species outnumbers the other species) which may suggest competition between the two species.

In reference to complexity-diversity relation, complexity has been shown to have a positive relationship with species diversity. For example, in studies of coral reefs [61] forest canopies [62], vegetated freshwater systems and soft bottom marine systems [63]. Habitat of higher structural complexity has been found to support more individuals and have greater diversity than less complex habitats.

Species diversity is the range of various species that are represented in a given community. Understanding this phenomenon enables ecologists to understand other biodiversity issues such as community stability, biological invasions, species coexistence, and detection of rare taxa. But comparison of different species abundance among communities can be difficult since communities are comprised of diverse species whose abundance profiles differ among communities. To solve this complexity, a number of diversity indices have been introduced. Namely Rank abundance curve, Shannon diversity, Simpson's diversity and Fisher's α. One of the commonly used measures of abundance is the **rank abundance curve**. These curves have helped to visualize species abundance distributions.

Rank abundance curve

It is a chart which has always been used by the ecologists to visualize **species richness** (number or count of the species in a community) and **species evenness** (how close in numbers each species are). It plots the species from the most to least abundant along the $x - axis$ while the $y - axis$ displays their relative abundance [64].

An example of a rank abundance curve is shown in Figure 2.5.

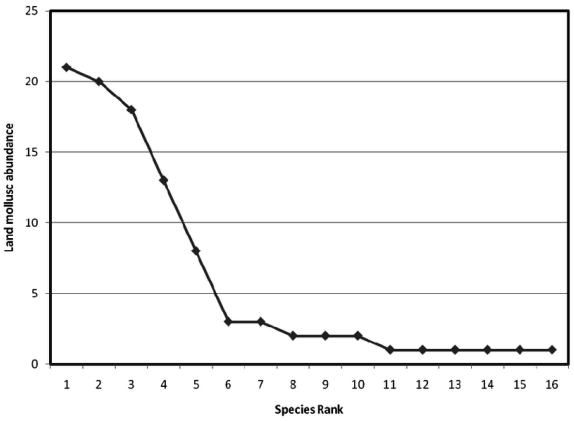


Figure 2.5: Rank abundance curve of land molluscs in Okpai swamp forest. Figure redrawn from [65]

Using rank abundance curves have its advantages: it provides a clear display of the contrasting patterns of species and it makes the species relative abundance clearly visible, especially when there are relatively few species.

Rank abundance curve displays the difference in species evenness and richness among species. Species richness is the number of species ranked. For instance, in figure 2.5 the total species ranked are 16 but only 4 species dominate the ecosystem.

Species evenness, on the other hand, is shown by the slope of the line that fits the graph. A steep slope shows assemblages with high dominance while shallow slope shows higher evenness implying that different species do not differ much in their abundances.

Productivity

Mathematically, productivity is the unit mass per unit volume per unit time. However, the total abundance of the species in the entire community is sometimes used as a surrogate for productivity: $\sum_i^S N_i$ where N_i is the species abundance of species i in community with S species.
In this work, I have used total biomass and productivity interchangeably where total biomass in this case total species living in a given area or of a biological community or group.

Competition intensity

The intensity of competition can be seen from two perspectives: the competitive effect that the species subjects to its interacting partners (henceforth competitiveness) and the competitive effect a species receives from its interacting partners (henceforth endurance). Competitiveness of a species is computed as the row sum of the community competition matrix elements while endurance is computed as the column sum of the community competition matrix elements.

2.8 Interaction switching

Species interactions have often been modelled using population dynamics models such as the competition model earlier illustrated in Section 2.5. However, most of these models have focused solely on the effect of these interactions to species abundance without considering adaptation mechanisms. Previous research has shown that species often switch their interaction partners either due to environmental effects or resources availability [27, 66].

There are various definitions of species interaction switching but in this study I base my definition on Peter Abrams definition. According to Abrams [67], species interaction switching is the ability of consumers to adaptively increase consumption of one resource at the expense of decreased consumption of the alternative resource.

Interaction switching has been a topic of interest among ecologists and evolutionary biologists over the years. Various forms of switching have been hypothesized. Namely: context-dependent species rewiring [16, 17], survival through selecting and switching interaction partners [28, 68], decision making based on profitability and encounter rate (abundance) [25], Wallace's the elimination of the unfit [30, 69] (henceforth I refer to as elimination switching) and Darwin's Survival of the fittest [16, 31] (henceforth optimization switching). In this thesis I focus only on two forms of switching: optimization switching and elimination switching.

(i) **Elimination switching**

This process of interaction switching was initially proposed by Alfred Russell Wallace as a process of natural selection. A species suppresses unbeneficial interactions by substituting them with new partners selected at random. This adaptive behaviour has been actualized for bipartite antagonistic networks [69] and bipartite mutualistic networks [30].

In their models, they solved the population dynamics numerically, such that, at each time step, a consumer selected randomly stops its interaction with the resource which least contributes to its per capita population growth rate. The consumer then initiates an interaction with another random non-interacting resource.

(ii) **Optimization switching**

This process of interaction switching was initially proposed by Herbert Spencer and Charles Darwin as a process of natural selection. In this switching procedure, a species switch to a new random interacting partner is accepted if and only the new interaction improves its per capita population growth rate. Recently, Suweis and his collaborators [31] have implemented this algorithm for mutualistic networks.

2.9 Summary

In this chapter, I gave an introduction to ecological networks by presenting the different types of these networks. In particular, I based the introduction using the mathematical formalism on the basics of graph theory by defining a network and how adjacency matrices determine the various types ecological networks.

Ecological networks are complex hence the need to have metrics for quantifying community structures and community functioning. Thus, I introduced selected community structure descriptors, linear stability measure and a metric for quantifying diversity. These descriptors, for instance, nestedness and modularity have been postulated as the key factors in promoting community structure and architecture. Also, understanding species diversity is crucial to understanding what maintains community structure.

In conclusion, I introduced species adaptive interaction switching as one of the factors highly attributed to promoting community structure and architecture. I placed specific interest on two commonly used forms of switching: Wallace's elimination of the unfit and Darwin's survival of the fittest.

Chapter 3

Single Community

3.1 Model Development

Based on the introduction to competition models in chapter 2, here I formulate a model which depicts the structural patterns of competitive community.

To develop my model for simulating population dynamics for multiple competing species I will use base case of a modified competitive Lotka-Volterra model.

From equation 2.6 I generalize the 2−species competition model into n number of species competing against each other. The population and growth rates are organized as vectors while the interaction $\alpha's$ as matrix. Then the equation of i^{th} species is given as:

$$\frac{dX_i}{dt} = r_i X_i \left(1 - \frac{\sum_{j=1}^{n} \alpha_{ij} X_j}{K_i}\right) \quad \text{for } i = 1, \cdots, X_n \tag{3.1}$$

The parameters r_i describe the intrinsic growth rates; K_i the carrying capacity of the ecosystem; α_{ij} shows the interactions between species, which describe the effect of species j on species i. If $\alpha_{ij} > 0$ the species j reduces growth of species i.

Competitive interactions happens when all $\alpha_{ij} > 0$ [5].

To enable us incorporate switching into my simulation, I modify Eq. 3.1 by separating the interaction coefficient α_{ij} into α_{ij} and β_{ij}.

$$\alpha_{ij} \rightarrow \alpha_{ij} \times \beta_{ij}$$

That is, the community matrix coefficients α_{ij} become a combination of β_{ij} the strength matrix coefficients and α_{ij} the interaction matrix coefficients.

The resulting model is given as:

$$f_i = \frac{dX_i}{dt} = r_i X_i \left(1 - \frac{\sum_{j=1}^{n} \alpha_{ij}\beta_{ij}X_j}{K_i}\right) \tag{3.2}$$

Interaction matrix coefficient $\alpha_{ij} = 1$ when species i and species j interact $(\alpha_{ii} = 1)$ and $(\alpha_{ij} = 0)$ represents no interaction. β_{ij} represents the competition coefficient, where β_{ii} represents the intraspecific competition strength. For species coexistence, β_{ii} should be greater than β_{ij}. All parameter values are non-negative.

Given an equilibrium solution X^*, the behaviour of this community at or very near to equilibrium is provided by its community matrix $\mathbf{M}$ [14], whose elements $m_{ij} = \frac{\delta f_i}{\delta X_i}\Big|_{X^*}$. Substituting in Eq. 3.2 here gives

$$m_{ii} = Xi^* r_i (1 - \sum_{j=1}^{n} \alpha_{ij}\beta_{ij}X_j^*) \tag{3.3}$$

$$m_{ij} = -\sum_{j \neq i} \alpha_{ij}\beta_{ij}X_i^* \tag{3.4}$$

I parametrized the community matrix M studied here as follows. First, community matrix is composed of interaction matrix A and competition strength matrix $\mathbb{B}$. I drew the non-zero diagonal elements of β_{ij} of the competition strength matrix from an half-normal distribution $N(0, \sigma^2)$. The diagonal elements $\beta_{ii} = 1$. The latter condition implies that differences between communities will only be due to the arrangement and strength of off diagonal elements [14]. The elements of interaction matrix A were drawn with probability C for non-zero elements.

3.2 Simulations

I numerically solved the above model (Eq. (3.2)) via Euler method. I employed a time step of 0.01 up to a total time of 100 at which the population dynamics appeared to stabilise. Initial population densities were randomly assigned between 0 and 1; intrinsic growth rates r_i assigned 0.5 and carrying capacities k_i fixed at standard values 1. The competition strength coefficients were randomly drawn following half-normal distribution with mean 0 and standard deviation σ. To ensure coexistence among species, I set the values of the intra-specific competition strength (i.e., β_{ii} for all species i) equal to 1. The off-diagonal elements of the interaction matrix were initialized randomly 0 and 1 values with 0 initialized with probability $1 - C$. The main diagonal entries set at 1 (represent intraspecific interaction).

A simulation was performed for each approximate connectance value ranging from 0.1 to 0.9 with a step of 0.05. The actual values of connectance are indeed slightly higher that these approximate values because of the diagonal elements a_{ii} forced to be equal to 1.

The interaction matrix was updated at each time step according the rules of elimination and optimization switching.

3.3 Adaptive interaction switching

I implemented the adaptive interaction switching in my resource competition model for depicting the population dynamics of multiple species competition network. The implementation followed the two different switching procedures: a switching by elimination of the interaction with the partner having the highest competitive effect, or a switching to a competing partner having a lower competitive effect. At each time step I incorporated interaction switching into the model by tracking the population dynamics of the species. By so doing I intend to track the stability by monitoring the lead eigenvalues of interaction matrix; productivity of community; level of nestedness and competitiveness.

In detail, I implemented the switching criteria as described in section 3.3.1 with a summarized illustration in figure 3.1.

3.3.1 Switching implementation

3.3.1.1 Elimination switching algorithm

At each time step, I randomly select a species and scrutinize the per capita effect of its competing partners on its population growth rate (i.e., checking all $\alpha_{ij}\beta_{ij}N_j$ for all the partners species j). The interaction that gives the highest competitive effect (say, species k) is dropped (i.e., $\alpha_{ik} = 0$) and switched to a randomly chosen species m which previously did not interact with species i (i.e., $\alpha_{im} = 1$). This switching criterion is like the switching procedures implemented by Zhang et al. [30] and Nuwagaba et al. [29].

A simplified algorithm of this rule is given as:

Algorithm 1 Interaction Switching rule

```
1:  procedure ELIMINATION SWITCHING RULE
2:      for all time steps do
3:          choose a species i randomly from the community matrix(M)
4:          pick the dominant competitor interacting with i-denote l
5:          if l ≠ i then
6:              randomly select the maximum in i except intraspecific partner.
7:          end if
8:          randomly choose a new species k not interacting with i i.e., α_ik = 0
9:          swap interaction between i and l to species i and k.
10:         implement Euler
11:     end for
12: end procedure
```

3.3.1.2 Optimization algorithm

At each time step, I randomly select an existing interaction between two species i and k. I then attempt to swap this interaction with another interaction between the same species i and a potential partner m. The interaction switch from (i,k) to (i,m) is accepted if and only if it does not lead to a negative growth in the population density of species i. Otherwise, species i looks for another potential partner to switch its interaction with until it exhausts all available partners.

A simplified algorithm of this rule is given as:

Algorithm 2 Optimization switching algorithm rule

```
1: procedure OPTIMIZATION SWITCHING RULE
2:     for all time steps do
3:         choose a species i randomly from the community M
4:         randomly select two species interacting with i, denote k and m
5:         swap the position of species k and m in interaction matrix and compute the
   growth rate
6:         if positive change in growth rate then
7:             accept the swap and interchange their competition strengths coefficients
8:         else if  change in growth rate is negative then
9:             repeat by selecting new m then
10:        end if change growth rate is positive.
11:        implement Euler
12:    end for
13: end procedure
```

A summarized version of the switching algorithms are illustrated below:

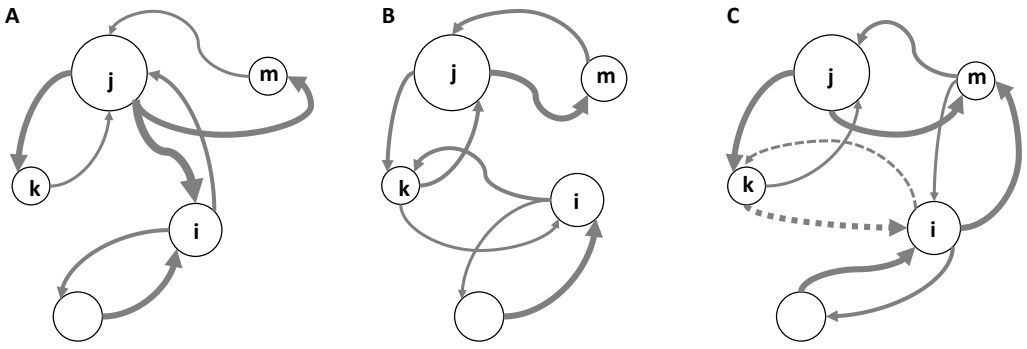


Figure 3.1: **Graphical illustration of the switching algorithms.** The size of the circle shows species abundance and the thickness of the arrows represents the competition strengths. (**a**) Non-switching case, species i interacts with other species. (**b**) Elimination switching, due to strong competition from species j, species i stops interaction with j and start new interaction with species k. For optimization switching, (**c**) species i switches to interact with k but species k doesn't improve species i per capita growth rate (represented by dotted line) then switch not confirmed, i switches to interact with new species m.

3.4 Simulation results

This are brief summary of the results I obtained from my analyses.

3.4.1 Relationship between network complexity, architecture, and stability

Productivity and evenness

Community productivity was computed based on the described criteria on Section 2.7.

Results show that there is negative relationship between productivity and connectance in switching and non-switching communities (Fig. 3.2(a)). Furthermore, adaptive interaction switching proves beneficial in promoting community productivity where both switching procedures depict better productivity than a non-switching community.

It can also be noted that under low to intermediate connectance (i.e., when the connectance ranges approximately from 0.1 to 0.8), a community under elimination switching procedure is more productive than one under optimization switching. In turn, in highly connected communities ($c > 0.8$), a switching via optimization turns out to provide the highest productivity (see appendix note A.4). Indeed, when a species switches its interaction via elimination, it can only switch to a new randomly chosen partner that did not previously interact with it. Thus, switching options become limited at high connectance. Contrastingly, when a species switches its interaction via optimization, choice of a new partner also

involves those species that are already competing with it. In that case, a switching corresponds to an interchange of competition strength.

Productivity is noted to be negativity related to standard deviation. There is a negative relationship between productivity and standard deviation with high productivity at low standard deviation value ($\sigma = 0.1$) and low productivity at relatively highly varied species strengths ($\sigma = 0.5$). This is evident in all the different community species populations (see appendix note Fig. A.4). Something to note also is the swap between elimination and optimization switching with elimination being highly productive at $\sigma = 0.1$ while optimization better at $\sigma = 0.5$ (see also appendix Fig. A.4).

As part of capturing effect of switching on diversity I measured species richness and evenness by using species rank abundance curve as described in Section 2.7. This has been implemented on *R* statistical software in *biodiversityR* package version 2.8-3 [70].

This results depict positive influence of switching on species evenness. Indeed, species rank-abundance curves show shallower gradients in both switching criteria as depicted by flatter graphs, compared to the non-switching case (Fig. 3.2(b)). This can be described as an increase in abundance of the rare species in community with interaction switching. Switching under elimination performs the best in promoting evenness between species abundance, especially for low connectance values. As connectance increases, species evenness is adversely affected: highly connected communities show less evenness in species abundances (see also appendix note A.5). Furthermore, all species could coexist through the simulations regardless of whether there was interaction switching or not.

Community stability

I quantified stability based on the description in Section 2.6 computed by taking the absolute value of the maximum real part of the eigenvalue obtained by finding the Jacobian of the community matrix.

For better analysis of the effects of complexity factors on stability I have visualized my results for a range of value of *connectance*, S and σ.

From the simulation results, adaptive interaction switching is evidently a catalyst towards a stable community structure. Indeed, community stability, measured as system resilience is enhanced in an environment where species can switch their interactions. Switching under elimination is the best procedure for promoting community resilience (Fig.3.2(c)) under low connectance (see also appendix note A.1). The system is more resilient at low connectance and community strength but tends to low stability as connectance and community strength increase. In figure A.1 for $\sigma = 0.5$, the system is unstable in non-switching but less stable for both switching algorithms. Community stability is also dependent on the species richness whereby at $S = 20$ it is highly stable but destabilizes at $S = 100$ (appendix

note A.1).

Nestedness

I quantified the level of nestedness using *bipartite* R package version 2.08 [71] on which NODF measure described in Section 2.2 has been implemented. This was computed to check on the influence of switching on the dominant and inferior competitors interactions. Unlike stability, nestedness is highly positively correlated with connectance with optimization switching performing better than both elimination switching and non-switching cases. Elimination switching and non-switching do not have any difference in community nestedness. Complexity measure (S) and competition strengths (σ) are not big factors in influencing nestedness as compared to its influence on stability and productivity (see appendix note A.6). Optimized communities are highly nested.

3.4.2 Competition intensity

As per my description on competition intensity measure in Section 2.7, my simulation results showed that there is a positive relation between competitiveness and species biomass (Fig. 3.3). In a non-switching environment, the competitiveness is lower compared to an adaptive switching environment due to adaptation which enable more species persistence even at high competitiveness levels. Thus, high competitiveness is associated with high productivity 3.3 (a). This shows that interaction switching plays a role in absorbing the competitive pressure a species receives in that at high competition intensity there is high productivity. In relation to species endurance, switching depicts high endurance scenario while non-switching cases have short endurance span Fig. 3.3 (b) .

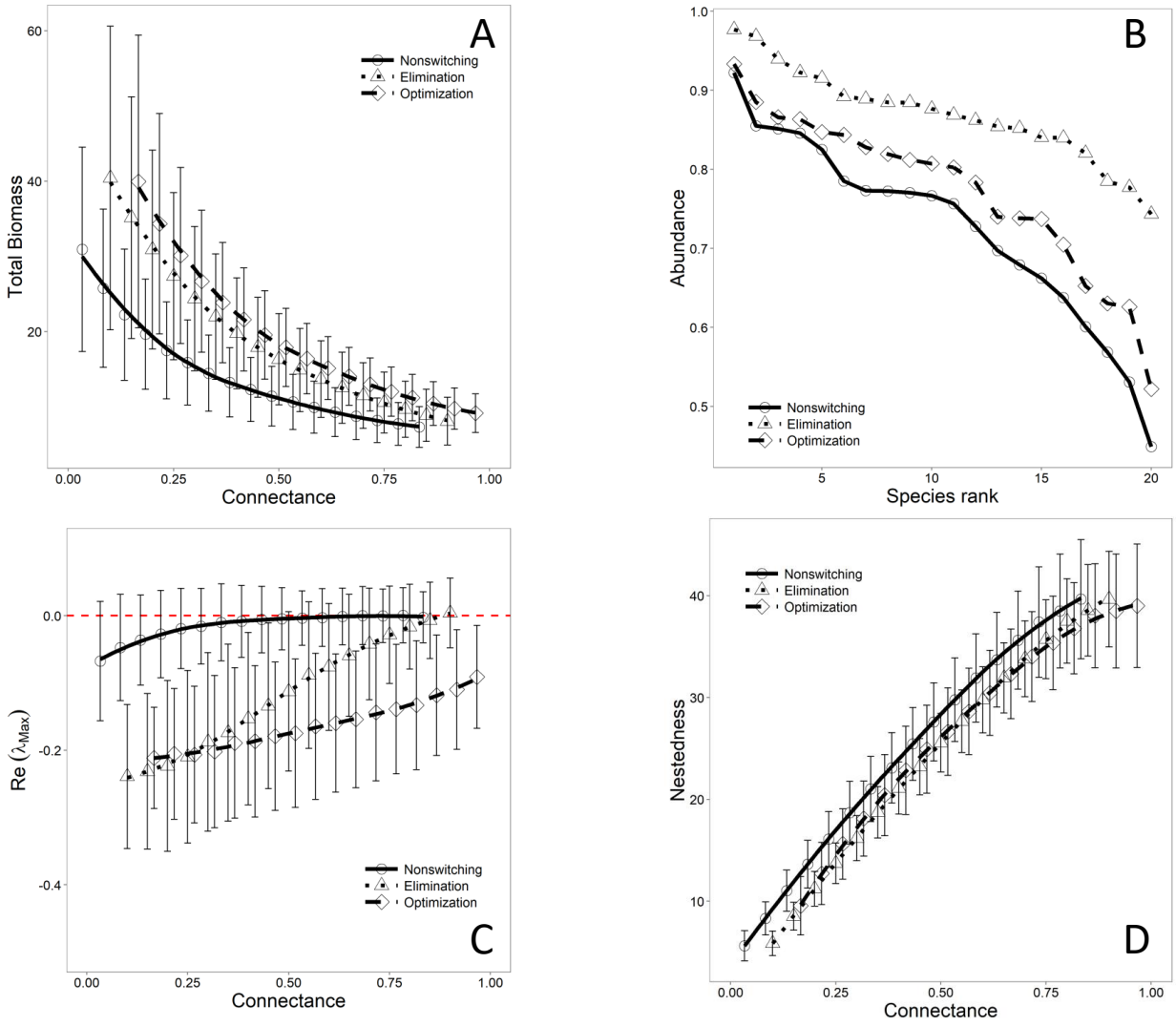


Figure 3.2: **Relationship between network complexity, stability, and architecture.** Simulations done for community with $S \in \{20, 50, 100\}$, $\sigma = 0.1$, $C \in \{0.1 - 0.9\}$. The points represent the average for 50 community networks analysed for each connectance values and the regression lines obtained using LOESS. The errors bars shows the spread of data points around the mean. (a) Total biomass versus connectance. Productivity is high at low connectance with a negative correlation between productivity and connectance. Productivity is enhanced through switching. (b) Rank abundance curves for selected connectance $(C = 0.5)$ and a community with 50 species. Switching positively influence species evenness and increase in abundance of rare species. (c) Stability versus connectance. System is highly stable at low connectance. Switching improves stability. (d) Nestedness versus connectance. Switching has no affect on nestedness.

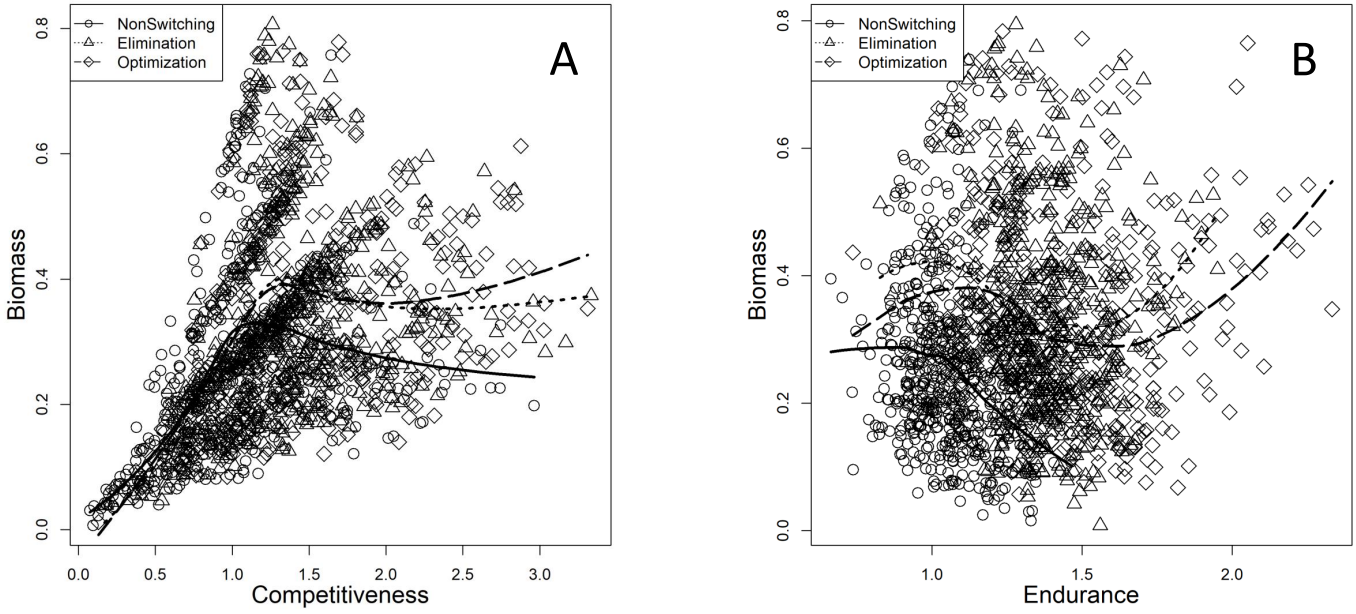


Figure 3.3: **Relationship between biomass, competitiveness and endurance.** Simulations done for community with $S \in \{20, 50, 100\}$, $\sigma = 0.1$, $C \in \{0.1 - 0.9\}$. The points represent the average for 50 community networks analysed for each connectance values and the regression lines obtained using LOESS. (a) Competitiveness vs biomass. Competitiveness computed as the row sum of the community competition matrix elements. Species competitiveness is positively correlated to biomass with switching enhances species competitiveness. (b) Endurance vs biomass. Endurance computed as the column sum of the community competition matrix elements. Switching is associated to increased endurance with non-switching cases having short endurance span.

3.4.3 Comparison with May's stability criteria

From the stability simulation results (Fig. 3.2(c)), I have illustrated that the system, destabilizes as $S, C,$ and σ increases but switching minimizes the complexity effect on stability.

Using the stability and productivity results, I conclude by comparing switching performance with May's complexity stability criterion given as:

$$\sigma\sqrt{(S-1)C} < \mu$$

.

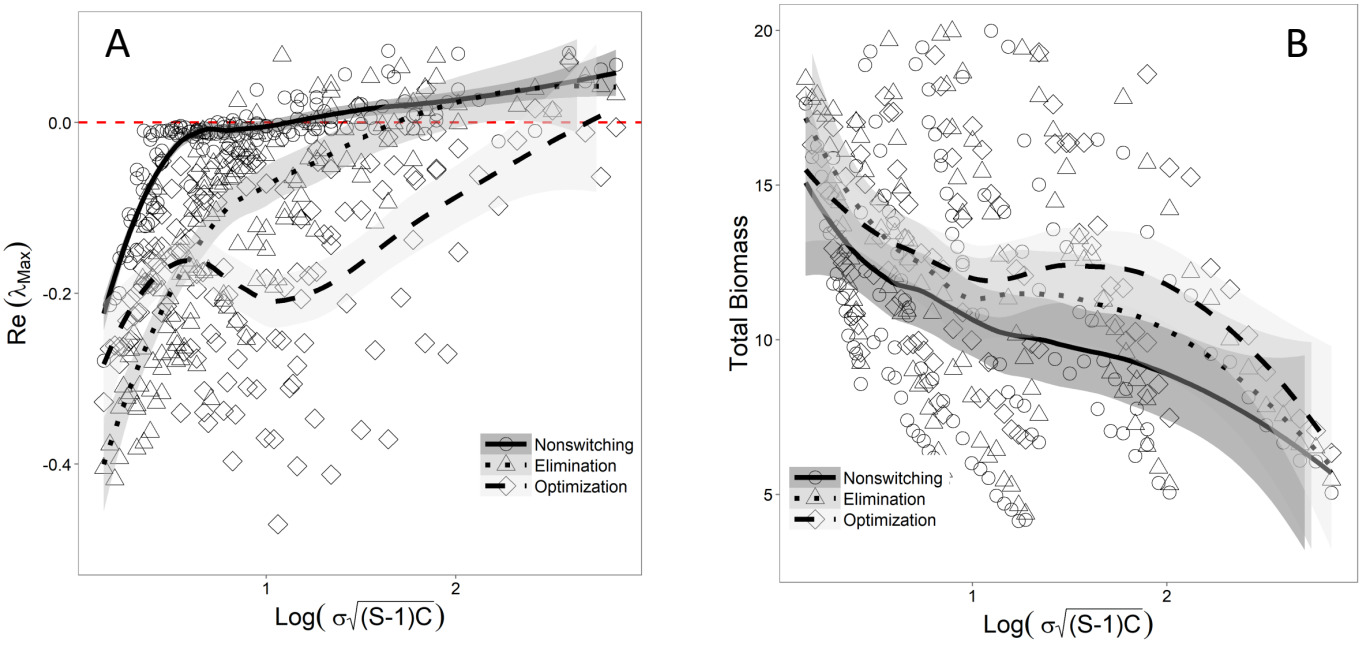


Figure 3.4: **Relationship between May's stability criteria $(\sigma\sqrt{(S-1)C})$, community stability (maximum real eigenvalue) and productivity.** (a) May's stability criteria versus community stability. Switching minimizes the destabilizing effect on complexity stability relationship. (b) May's stability criteria versus productivity(total biomass). Switching enhances community productivity. Optimization switching performs better in minimizing destabilizing effect and improving productivity. Regression curves were obtained using LOESS curve fitting.

As per May criteria, increase in species complexity decreases stability but incorporating switching into my model the destabilizing effect is minimized. Both switching algorithms employed in my model have a slower rate of destabilization with optimization performing better than elimination.

For productivity, switching enhances productivity (total biomass) compared to non-switching with optimization high productive than elimination.

Non-switching formulation concurs to the May's hypothesis that a system is stable up to a certain threshold quantified using the criterion $\sigma\sqrt{(S-1)C} < \mu$. On the other hand, switching has push effect on the threshold. Using initial parameter formulation, in the Section 3.4.4 I develop a new stability criterion incorporating switching effect.

3.4.4 Stability criteria

Here I formulate a new stability criterion based on the switching influence on species interaction strengths σ. Robert May [1] introduced a complexity-stability measure, $\sigma\sqrt{sc} < \mu$ where σ is the standard deviation of species interaction strengths, s number of species, c

the connectance level, and μ the intraspecific competition strength.

In developing the criterion, May used random matrix theory where species interactions are represented in a community matrix, M defined by competition strength matrix B and interaction matrix A (from 3.2). Off-diagonal elements, B_{ij} are generated to follow a half-normal distribution with mean zero and variance σ^2 i.e., $\beta_{ij_{i\neq j}} \sim \left|N(0,\sigma^2)\right|$. Recall, elements of interaction matrix A are generated with probability $1-C$ for the non-interacting species.

Let $s(s-1)$ be n. Thus, implies that the proportion of realised interactions in the community is n^*c representing the community connectivity (henceforth denoted m).

I start by defining half-normal probability density function (pdf) given as:

$$f_Y(y;\sigma) = \frac{\sqrt{2}}{\sigma\sqrt{\pi}} \exp^{-\frac{y^2}{2\sigma^2}}, \quad y \geq 0 \tag{3.5}$$

where by the cumulative distribution (CDF) is

$$F_Y(y;\sigma) = \int_0^y \frac{1}{\sigma}\sqrt{\frac{2}{\pi}} \exp^{-\frac{x^2}{2\sigma^2}}\, dx \tag{3.6}$$

Using change-of-variables $t = x/(\sqrt{2\sigma})$, equation 3.7 can be written as

$$F_Y(y;\sigma) = \frac{2}{\pi}\int_0^{y/\sqrt{2\sigma}} \exp^{-\frac{t^2}{2\sigma^2}}\, dt = erf(\frac{y}{\sqrt{2\sigma}}) \tag{3.7}$$

where erf is the error function. A graphical representation of the CDF:

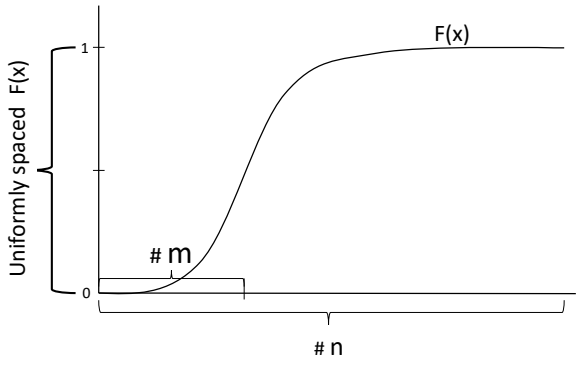


Figure 3.5: Cumulative distribution curve

I postulate that the image of the $n, F_{n's}(X)$ and $m, F_{m's}(X)$ generated are uniformly spaced CDF values such that $F(X_m) = \frac{m}{n} = c$.

My aim is to illustrate the influence of switching on the species interaction strengths (σ) on the May's stability criteria by deducing σ_m of the m random variables explained by community connectance c.

From Eq. 3.7 I use Taylor expansion to approximate the cumulative density function (CDF). Without considering the coefficient of the function, the Taylor expansion of an exponential function $\exp^{-\frac{x^2}{2\sigma^2}}$ is

$$\exp^{-\frac{x^2}{2\sigma^2}} = \sum_0^\infty \frac{(-1)^n x^{2n}}{2^n n! \sigma^{2n}}$$

Therefore,

$$\begin{aligned} F_Y(y;\sigma) &= \int \frac{1}{\sigma}\sqrt{\frac{2}{\pi}} \sum_0^\infty \frac{(-1)^n x^{2n}}{2^n n! \sigma^{2n}} dx \\ &= \frac{1}{\sigma}\sqrt{\frac{2}{\pi}} \sum_0^\infty \frac{(-1)^n x^{2n+1}}{2^n n! \sigma^{2n}(2n+1)} \\ &= \frac{1}{\sigma}\sqrt{\frac{2}{\pi}} \left(x - \frac{x^3}{6\sigma^2} + \frac{x^5}{40\sigma^4} \right) + O(x^7) \\ F(x) &= \sqrt{\frac{2}{\pi}} \left(\frac{x}{\sigma} - \left(\frac{x}{\sigma}\right)^3 \frac{1}{6} + \left(\frac{x}{\sigma}\right)^5 \frac{1}{40} \right) + O(x^7) \end{aligned}$$

Since X is a random variable generated by a continuous distribution then the variance is given by

$$\begin{aligned} Var(X) = \sigma^2 &= \int (x-\mu)^2 f(x) dx \\ &= \int x^2 f(x) dx - \mu^2 \end{aligned}$$

I can express $\int x^2 f(x) dx$ in terms of cumulative function by integration by parts i.e., let $u = x^2$ and $dv = f(x)dx$. Then $du = 2xdx$ and $v = F(x) - 1$. Therefore,

$$\int x^2 f(x) dx = x^2(1 - F(x))\Big|_0^\infty + \int 2x(1 - F(x)) dx$$

Then

$$Var(X) = \int 2x(1 - F(x)) dx - \mu^2$$

where $F(x) = \sqrt{\frac{2}{\pi}} \left(\frac{x}{\sigma} - \left(\frac{x}{\sigma}\right)^3 \frac{1}{6} \right)$ up to 3-rd order.

Since $F(X_m) = C$, then $X_m = F^{-1}(C)$ given as

$$X_m = \sqrt[6]{\frac{\pi}{2}} \sqrt[3]{\frac{\sqrt{9\pi\sigma^6 c^2 - 16\sigma^6}}{\sqrt{\pi}} - 3\sigma^3 c} + \frac{2\sqrt[6]{\frac{2}{\pi}}\sigma^2}{\sqrt[3]{\frac{\sqrt{9\pi\sigma^6 c^2 - 16\sigma^6}}{\sqrt{\pi}} - 3\sigma^3 c}}$$

Considering 1^{st} order of $F(x)$ I have

$$X_m = c\sigma\sqrt{\frac{\pi}{2}}$$

In my case μ is zero, then the variance would be:

$$\begin{aligned}
Var(X_m) &= \int_0^{X_m} 2x\left[1-\sqrt{\frac{2}{\pi}}\left(\frac{x}{\sigma}-\left(\frac{x}{\sigma}\right)^3\frac{1}{6}\right)\right]dx \\
&= \int_0^{X_m} 2x-\sqrt{\frac{2}{\pi}}\left(\frac{2x^2}{\sigma}-\frac{2x^4}{6\sigma^3}\right)dx \\
&= x^2-\sqrt{\frac{2}{\pi}}\left(\frac{2x^3}{3\sigma}-\frac{2x^5}{30\sigma^3}\right)\Bigg|_0^{X_m} \\
&= X_m^2-\sqrt{\frac{2}{\pi}}\left(\frac{2X_m^3}{3\sigma}-\frac{2X_m^5}{30\sigma^3}\right) \\
&= \left(c\sigma\sqrt{\frac{\pi}{2}}\right)^2-\sqrt{\frac{2}{\pi}}\left\{\frac{2}{3\sigma}\left(c\sigma\sqrt{\frac{\pi}{2}}\right)^3\right\} \text{ for 1-st order} \\
&= c^2\sigma^2\pi\left(\frac{1}{2}-\frac{c}{3}\right)
\end{aligned}$$

Therefore, the postulated stability criteria is

$$\underbrace{c\sqrt{\pi\left(\frac{1}{2}-\frac{c}{3}\right)}\sigma}_{\sigma_m}\sqrt{c(s-1)} < \mu \tag{3.8}$$

Comparing with the May's stability criteria and fully connected community I have

$$\text{Fully Connected} \quad : \quad \sigma\sqrt{(s-1)} < \mu \tag{3.9}$$

$$\text{Partially Connected} \quad : \quad \sigma\sqrt{(s-1)} < \mu c^{-\frac{1}{2}} \tag{3.10}$$

$$\text{Switching} \quad : \quad \sigma_m\sqrt{(s-1)} < \mu c^{-\frac{3}{2}} \tag{3.11}$$

$$\textit{where } \sigma_m = \sigma\sqrt{\pi\left(\frac{1}{2}-\frac{c}{3}\right)}$$

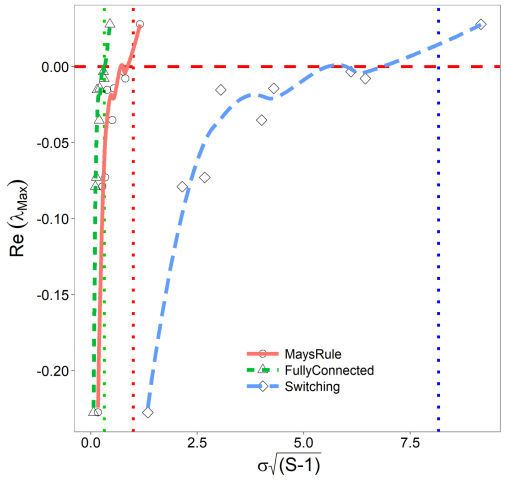


Figure 3.6: Numerical comparison of stability criteria. Green, red and blue dotted vertical lines are stability thresholds for fully connected systems, May's criteria and switching communities respectively. For fully connected $(C = 1)$ community stability threshold is reached faster compared to a partially connected community (May's criteria) and in a switching community. The graph confirms the switching influence on the May's criteria by pushing the stability threshold. The graph is for a community with 100 species and their competition strength is $\sigma = 0.1$.

3.5 Summary

In this chapter, I formulated a single community modified Lotka-Volterra model and investigated the impact of species interaction switching on the complexity-stability debate. I carried out a theoretical explanation of stability and gave a parametrization summary. I also illustrated on switching implementation and showed key insights from my simulation.

From the simulation analysis, it suffices to say that switching is a enhances species productivity both in a elimination switching community and optimization switching community. Switching improves the overall community productivity with a negative relationship with connectance. Competitive species switching tends to be more productive in a less connected community. Species evenness is also improved in a switching community thus switching is of great influence in ensuring equalness in species abundances thereby minimizing dominant species impact on inferior species. Switching enables thriving of the less dominant counterpart. This is evident at low community connectivity.

Stability is one of the crucial factors which have featured largely in the complexity-stability debate. Researchers have tried to unearth this paradox. From the results species interaction switching improves stability. Switching presents a better version of minimizing the destabilizing effect of complex communities. Connectance impacts stability effects in a community with low connected community being highly stable but the community gradually destabilizes with increase in connectance, interspecific interaction strength, and species

richness.

In conclusion on this chapter, I have summarized the whole simulation results by developing a new complexity-stability measure, $\underbrace{c\sqrt{\pi\left(\frac{1}{2}-\frac{c}{3}\right)}\sigma}_{\sigma_m}\sqrt{c(s-1)} < \mu$ which factors in switching influence on the existing May's stability criterion.

Chapter 4

Metacommunity

4.1 Introduction

In this chapter, I expand species interaction from single community (chapter 3) to multiple communities connected by dispersal. This is referred to as metacommunity. According to Leibold et al. [72], metacommunity is defined as a set of discrete communities partially connected through movement of individuals from other local communities or a regional species pool of multiple potentially interacting species as illustrated in Fig. 4.1. Alternatively, a metacommunity is a set of spatially distributed local communities connected via dispersal and hence influenced by recolonization and extinction events [73]. This set of discrete communities has often been referred to as microsites or localities or patches [36, 38, 74–76]

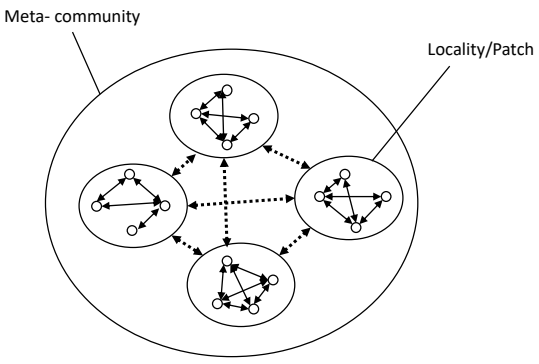


Figure 4.1: **An illustration of a metacommunity composed of localities.** The dotted arrows represent species movement from one locality to another through dispersal and the solid arrows indicate species interaction within a locality.

There is considerable body of work on the metacommunity theory revolving on community stability. These studies use diverse mechanisms each showing that dispersal has a potential to stabilize community interactions and improve on regional biodiversity [19, 36, 77–81].

With reference to competitive interactions, Amarasekare et al. [36, 79] in their work have shown that spatial competition models are crucial for community diversity maintenance because inferior competitors can easily persist in spatially distributed communities.

However, all of these studies are restricted to rather simple community with few species, and I could hardly extrapolate them to the more complex configurations found in nature [80]. Consequently, it is crucial to understand whether stability in a metacommunity follows the insights from study of simple independent communities.

In order to model metacommunity dynamics I incorporate species spatial flows into a single community model formulated in chapter 3 (see Eq. 3.2). I consider an homogeneous case where species have an equal dispersal rate from one patch to another depicting a spatially implicit model.

This chapter is divided into four main sections. The first section formulates the modified multipatch Lotka-Volterra model where I incorporate species spatial flows to my chapter 3 model. Similar models have previously been introduced through the works of Gravel et al. and Michio and Kondoh. In the second section I describe the stability analysis of a metacommunity by focussing on the structure of the Jacobian matrix. The third section describes how I analysed the model numerically using the Euler method while the fourth section of this chapter covers the results from the simulations. This last section is subdivided to capture the influence of dispersal and the combined influence of dispersal and switching. In both subsections, I focus on stability and productivity. I conclude the chapter by giving a summary.

4.2 Methods

4.2.1 Multispecies Multipatch Lokta-Volterra Model

Consider a competition metanetwork of n patches in which each pair of species i and j $(i, j \in 1, \cdots, S)$ are connected by competitive interaction with probability C. The population dynamics are defined using the following ordinary differential equation:

$$\frac{dX_{il}}{dt} = \underbrace{X_{il} r_{il}\left(1 - \frac{\sum_{j=1}^{S} \alpha_{ijl}\beta_{ijl}X_{il}}{K_{il}}\right)}_{\text{Our chapter 3 model (modified Lotka-Volterra model)}} - e_{il}X_{il} + \sum_{k=1(k\neq l)}^{n} \psi_{ilk}e_{ilk}X_{ik}$$

where $X_{il}(l = 1, \cdots, n)$ is the abundance of species i in patch l, r_{il} the intrinsic growth rate of species i in patch l, α_{ijl} the interaction coefficient between species i and species j in patch l, β_{ijl} the competition strength coefficient of j on i in patch l. e_{il} is the dispersal rates of species i from patch l and ψ_{ilk} is mortality rates of species i from patch k to l. I further simplified the model by combining $e_{il}X_{il}$ and $\psi_{lk}e_{ik}X_{ik}$ as both collectively form the dispersal cost and denoted ρ_{ilk}. Thus my model is simplified as

$$\frac{dX_{il}}{dt} = X_{il} r_{il} \left(1 - \frac{\sum_{j=1}^{S} \alpha_{ijl} \beta_{ijl} X_{il}}{K_{il}}\right) + \sum_{k=1}^{n} \rho_{ilk} e_{ilk} X_{ik} \tag{4.1}$$

4.2.2 Metacommunity stability analysis

To understand how species spatial flows might influence on the stability, I expand May's approach by looking at the structure of the Jacobian matrix. I considered the technique of local stability analysis as described in section 2.6 and be comparable to May's work.

The Jacobian matrices are obtained by linearising at feasible equilibrium the system of equations 4.1. A Jacobian matrix hence describes the direct interactions among all pairs of populations near this equilibrium. As indicated in section 2.6, the real part of the dominant eigenvalue indicates stability, and when negative, means the system is stable.

According to Gravel's approach the Jacobian matrix of the metacommunity can be broken-down into a sum of the intraspecific density matrix, dispersal matrix and local Jacobian matrices.

J= M+D+A

where **M** is the intraspecific density dependence diagonal matrix with value 1 along the main diagonal and 0 elsewhere; **D** is a matrix representing the dispersal among localities; and the matrices A form the diagonal blocks of J. The local Jacobian matrices describing interspecific competitions within each local community.

The analysis of the Jacobian **J** gives us the stability criteria threshold for metacommunities.

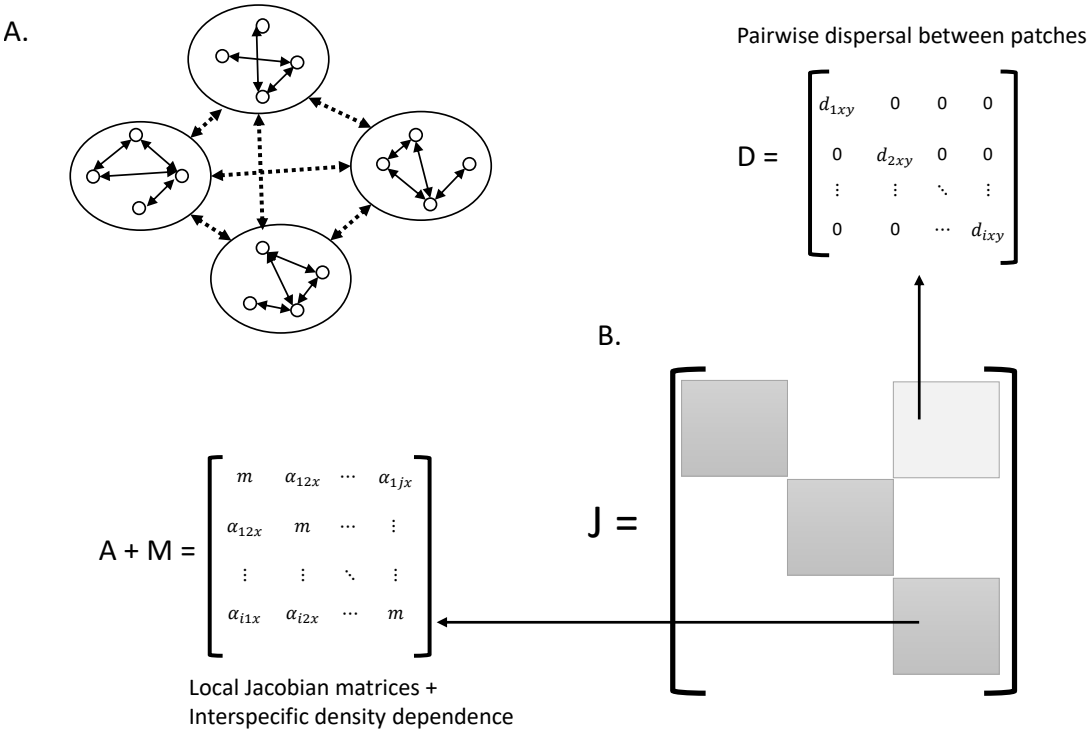


Figure 4.2: **Jacobian matrix of a metacommunity. (a)** Spatial network depicting the dynamics of a metacommunity. The dotted arrows represent species movement from one patch to another through dispersal. **(b)** shows the Jacobian matrix made up as a combination of submatrices **A, M** and **D**. Figure redrawn from Gravel et al. [78]

My proposed model 4.1 is only valid when the dispersal rate is low and the metacommunity is large, both in size S and in number of patches n. Using this insights Gravel et al [78] derived a simplified stability criterion:

$$\sigma\sqrt{C(S-1)} \leq m + d \tag{4.2}$$

where m and d represent the intraspecific interference and dispersal rate; S, C, and σ are number of species, the connectance and the average community strength.

Simulation

I numerically solved equation 4.1 using Euler method. I employed a time step of 0.01 up to a total time of 100 at which the population dynamics appeared to stabilize. Initial population densities were randomly assigned between 0 and 1, intrinsic growth rate r_{il} assigned

0.5 and carrying capacities K_{il} fixed at 1. The competition coefficients β_{ijl} were randomly drawn from an absolute normal distribution with mean 0 and variance σ^2 while the interaction matrix coefficients α_{ijl} are binary variables assigned 1 with probability C. I implemented my model using 3 localities each with 100 species connected via dispersal rate of 0.2 and mortality rates of 0.5. Furthermore, I included the switching algorithms into the model to explore a combined effect of switching and dispersal in metacommunity. Implementation of switching algorithms was done as per the description in Chapter 3 Section 3.3.

4.3 Results

Effects of dispersal rate on community stability

Using the random community matrices, I illustrate using eigenvalue distribution described in Section 2.6 the influence of dispersal on the stability. The eigenvalue distribution shows a shift of the eigenvalues to more negative values with increased dispersal rate (Fig. 4.2).

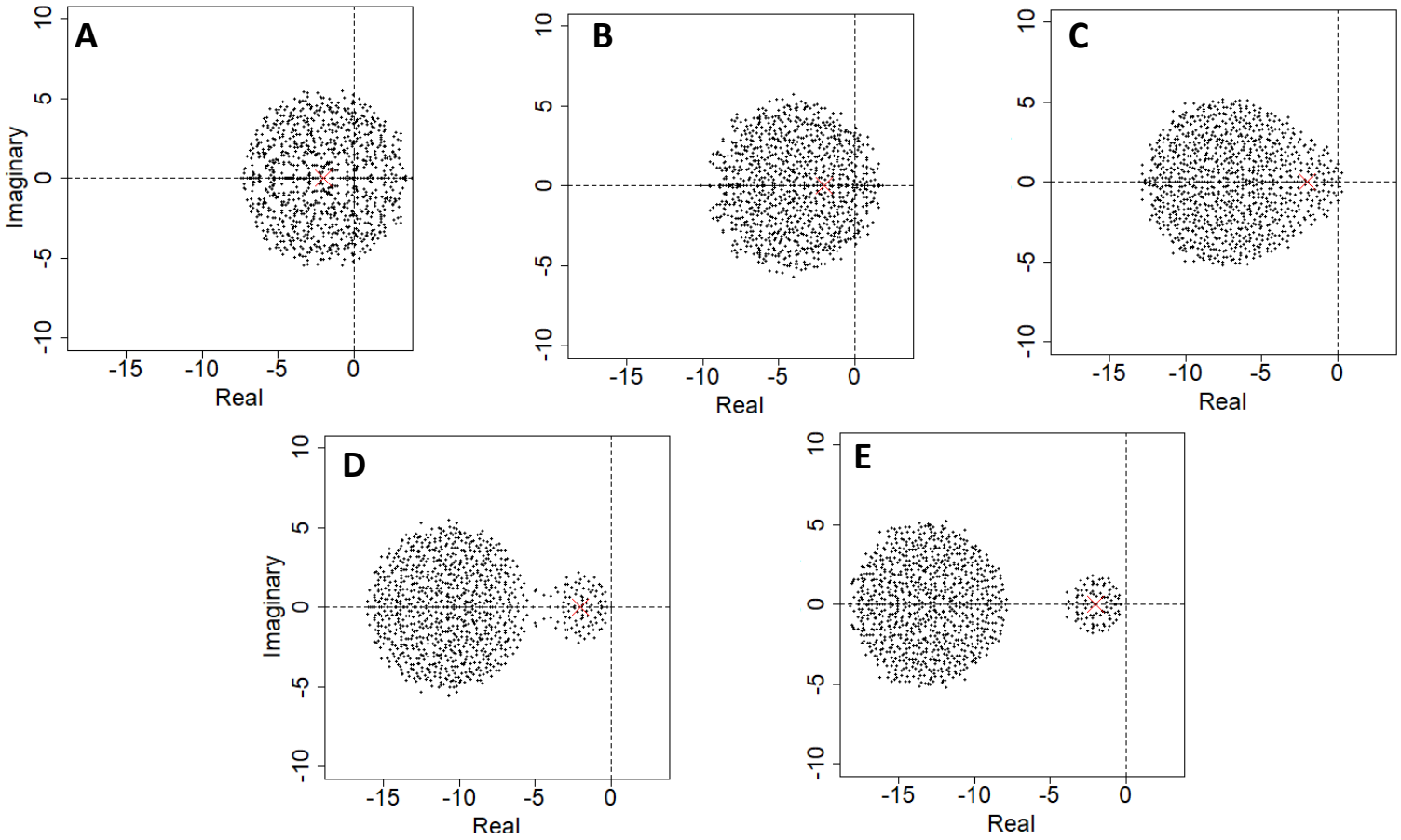


Figure 4.3: **Eigenvalue distribution of the community matrix M in the complex plane.** Parameters: $S = 100$, $\sigma = 1$, $C = 0.2$, $n = 10$ and **(a)** d = 0, **(b)** d = 2, **(c)** d = 5, **(d)** d = 8, **(e)** d = 10. Off-diagonal elements of the community matrix M are drawn from a normal distribution. The red stars indicate the position of centres of eigenvalues distribution.

To illustrate the influence of dispersal on the community stability, I compare single community stability (see Eq. 3.2) and the metacommunity stability (see Eq. 4.1) before considering switching effect.

Metacommunity without switching behaviour

Figure 4.4 shows that dispersal improves community productivity and stability.

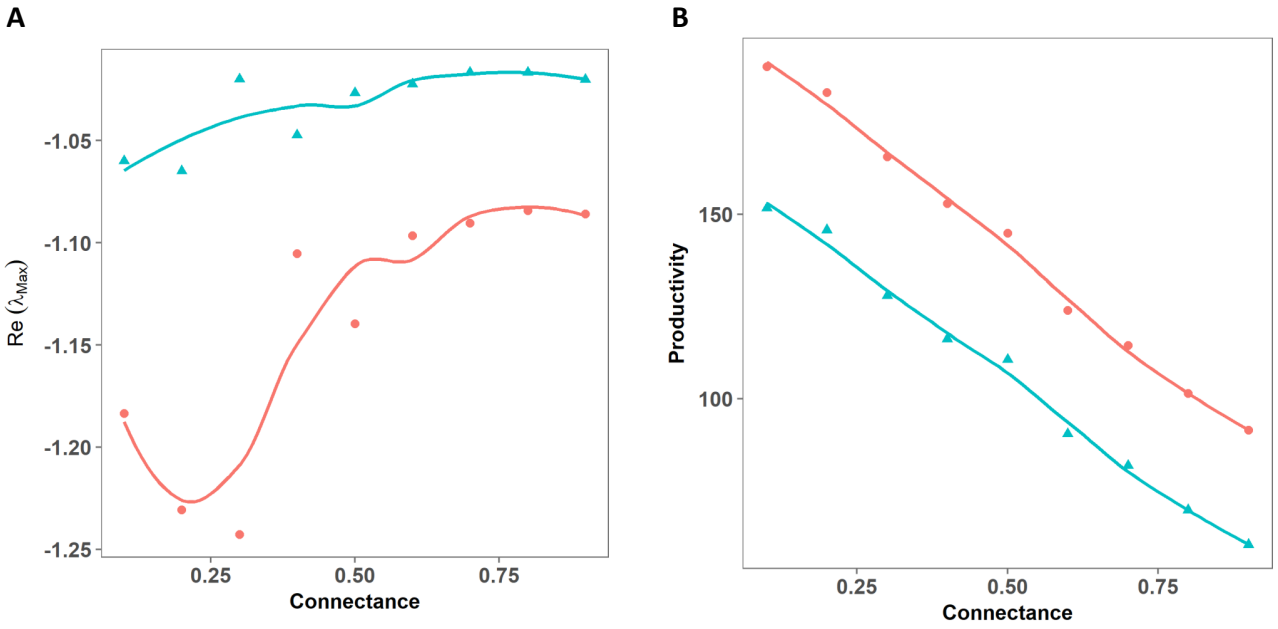


Figure 4.4: **Effect of dispersal on community stability and productivity. (a)** shows the influence of species movement on overall community stability. **(b)** illustrates the influence of dispersal on productivity. I analysed a metacommunity with 5 localities and 100 species each. The red lines show the case of a metacommunity with $d = 0.2$, while the blue lines are for isolated communities ($d = 0$).

This result confirms previous findings on the positive effect of dispersal on community stability and productivity [36, 78].

Metacommunity stability with switching behaviour

To justify the influence of a combined switching-dispersal effect on the complexity-stability debate I have visualized my results based on a metanetwork with interaction switching model of 5 localities, connected by dispersal. To capture the complexity factor I considered each locality composed of 100 species, *connectance* ranging from 0.1 to 0.9, the standard deviation of interaction strength, $\sigma = 0.2$ and dispersal rate fixed at 0.2.

Community stability has improved when I consider both dispersal and switching (Fig. 4.5). From figure 4.4, I showed that metacommunities are more stable than isolated communities but with an inclusion of switching to a metacommunity model, the community becomes even more stable.

As per chapter 3 results, community destabilizes with increased complexity whereas considering both switching and dispersal effect minimizes the destabilizing effect of complex-

ity.

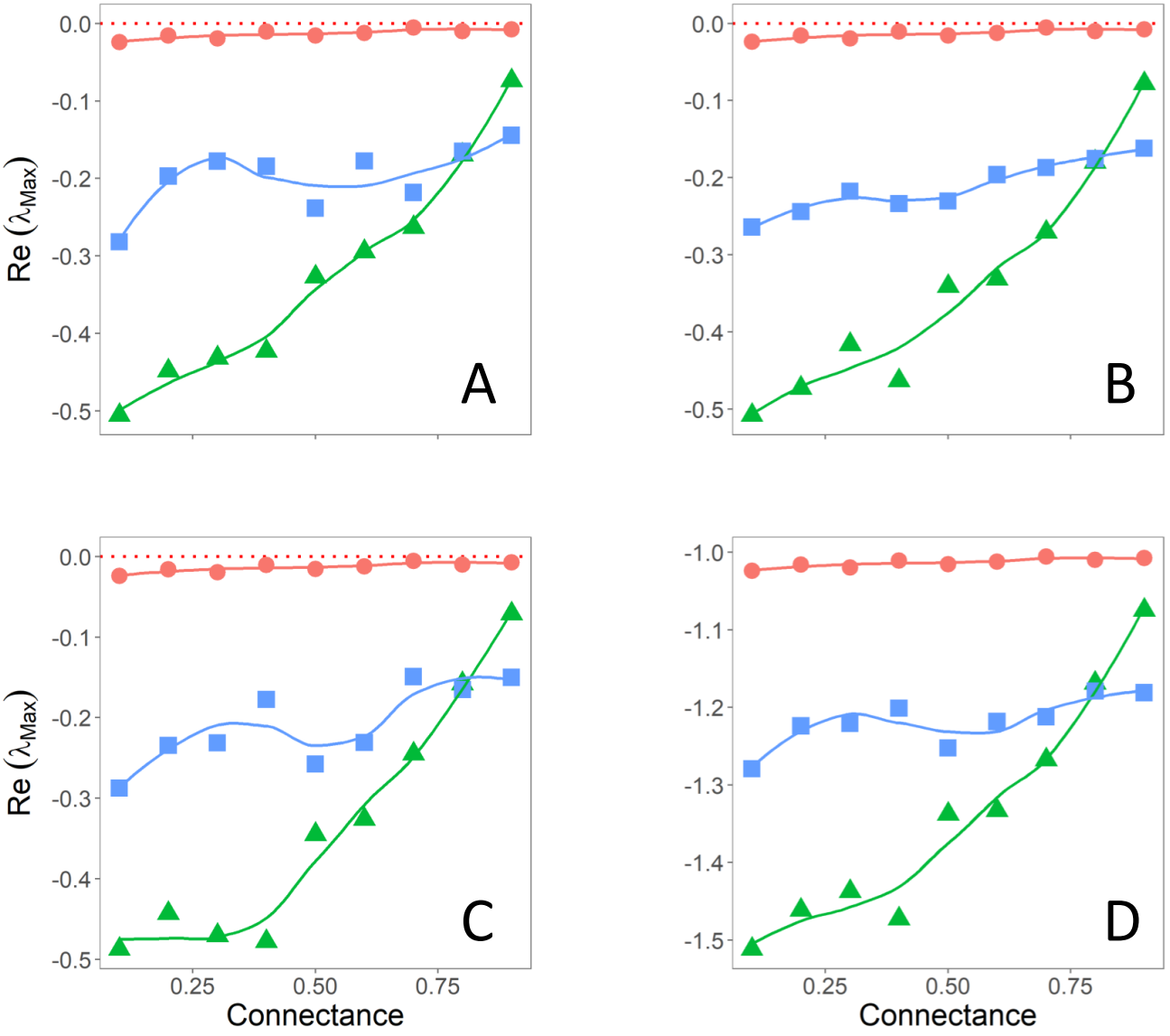


Figure 4.5: **Stability of a metacommunity with switching. (a),(b),(c)** shows community stability in different localities. **(d)** global stability. In each independent patch $S = 100$, $d = 0.2$. Red solid line represents non-switching case; green line is for elimination switching and blue is for optimization switching. Both switching behaviours reflect improved stability compared to a non-switching case.

Metacommunity productivity with switching behaviour

In relation to community stability, metacommunities allow more species persistence implying increase in species richness. More species persistence translates to improved commu-

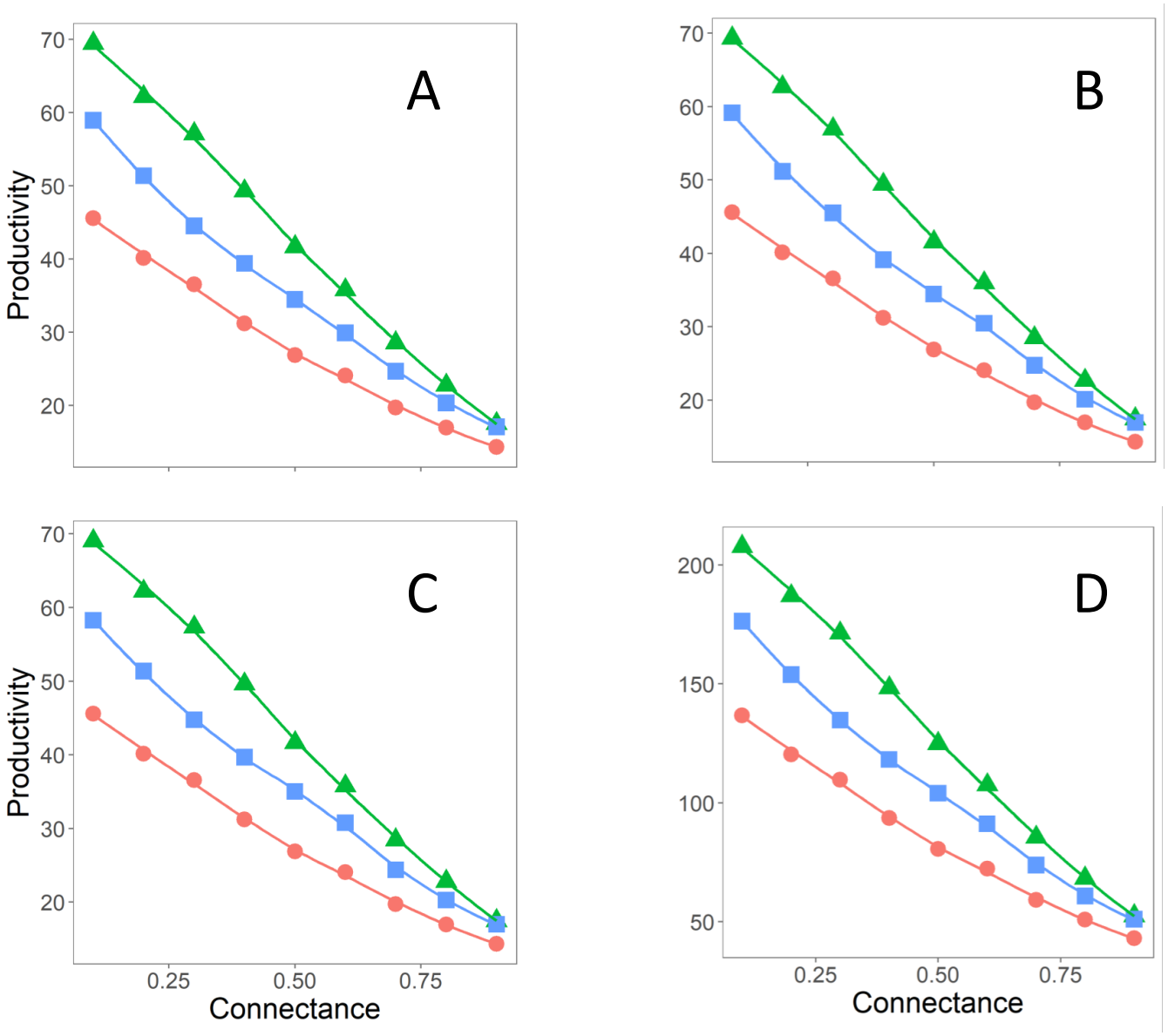


Figure 4.6: **Productivity of a metacommunity with switching. (a),(b),(c)** community productivity in different localities of 100 species each ($S = 100$) with dispersal rate $d = 0.2$. **(d)** global productivity. Red solid line represents non-switching case; green line is for elimination switching and blue is for optimization switching. Both switching behaviours reflect improved productivity compared to a non switching case.

nity abundance as compared to single community species richness. Figure 4.6 shows that a combined switching and spatial flows translates to increase in abundance, thus productivity.

Generally, both switching algorithms give higher productivity results compared to a non-switching case.

4.4 Summary

In this chapter I have studied the impact of a combined dispersal-switching on a multi-patch multispecies system. I used the approach employed by Gravel et al. [78] to analyse stability where species per site interactions are considered as diagonal blocks in the meta-community matrix. In comparison to isolated patches I provided a broader perspective.

My analysis confirms that dispersal generally improves community stability (see Fig. 4.4) which concurs with previous findings [78–80]. A deeper analysis into a combined dispersal-switching positively affects on community stability hence a new dimension to complexity-stability debate.

Moreover, community productivity is improved in metacommunities compared to single patches. This improved productivity and species persistence could be attributed to other patches offering refuge in case of a disturbance (such as wild fires, floods) namely in one of a neighbouring patch. This can be attributed to the source and sink dynamics orchestrated in a metacommunity. Less competitive species have options to immigrate to friendlier patches whenever stiff competition ensues.

Metacommunity species dynamics asserts the species spatial flow effects. Switching and dispersal illustrates a new point of view into the May's stability debate. However, communities in nature are not entirely homogeneous but rather heterogeneous. In each locality, species exhibit differential responses to the environment and covariance between the environment. Heterogeneity was however out of the scope of this thesis.

Chapter 5

Discussion and Conclusion

5.1 Discussion

Species diversity has been a great topic of interest to ecologists who endeavour to understand the role of biodiversity in ecosystem maintenance [5, 6] . Results from my study confirm that switching and spatial dynamics play a significant role in enhancing species richness and evenness by facilitating multispecies coexistence. My models indicate that low community connectance in competitive ecosystem depicts high productivity and high species evenness hence improved biodiversity. This increased abundant nature of rare species is associated with the adaptive effect of deciding whom to interact with. The increased species evenness illustrates an equal community where inferior or rare species coexist with the dominant species, an important feature of adaptive interaction switching. This agrees with other theoretical studies that found that switching enables species fluctuation without necessarily going to extinction [29, 68].

The first part of my analysis follows May's formalism to facilitate the comparison with his work and various studies that have employed random matrix theory. I further incorporated interaction switching and species spatial movement hence drawing a new perspective towards the complexity-stability debate. My analysis reveals that switching has a stabilizing effect on the Jacobian matrix and its corresponding eigenvalues. Based on May's criterion, a community is stable up to a certain stability threshold, which depends on the two factors: (1) community interspecific strength, (2) and the intraspecific competition strength. My analysis shows that switching moves the distribution of most of the eigenvalues towards more negative values. These results make a greater intuitive sense that switching minimizes the interspecific strength implying a reduced radius of the eigenvalues distribution hence stability. Similar outcome was replicated by spatial dynamics effect on stability (see Fig. 4.3 and appendix Fig. A.2), confirming previously done theoretical studies [78].

Furthermore, my results depicted a negative relationship between connectance and stability agreeing with previous research that also found an inverse relationship between complexity and stability [1, 6, 14, 31]. For instance, Kondoh [16] showed that the classic

negative complexity-stability relationship in static food webs [1] does not necessarily hold. This was further emphasized by Beckerman et al. [44] and Petchey et al. [82] by predicting food-web stability using interaction switches. Both single and metacommunity models outcomes depicted a highly stable community at low connectance with a destabilizing effect with increased connectance. These observations are consistent with the accepted hypothesis that switching enhances food web stability [16, 44, 83]. Nonetheless, the introduction of switching and species spatial flows minimized this destabilizing effect of complexity. Competitive communities are highly nested with increased connectance which has been coined to enhance resilience. From this results, interaction switching proves a strong force for stabilizing and structuring communities [17, 29, 30].

This switching criterion employed with other studied factors such as evolutionary processes and species complexities [16] is driving force towards ideal network architecture [29, 30]. For example, in mutualistic networks, switching of interaction partners to enhance relative benefit can give rise to the nested architecture [30]. Also, an antagonistic model incorporating an interaction switch can also lead to nestedness of bipartite food webs [28] consistent to real networks. Based on my results, the positive relation between nestedness and connectance, the high productivity and species evenness, and improved community resilience further illustrate the influence of switching in strengthening community architecture [19, 21, 29, 31]. In addition, under optimization, the species maximized the efficiency of resource consumption and minimize extinction possibilities which concur with preceding research [6, 25, 30]. This allows us to elucidate that interaction switching is a crucial factor in shaping the architecture of ecological networks.

In this study, I have provided a methodology for introducing adaptive behaviours into classic Lotka-Volterra model of ecological communities by allowing species to readjust its competition partners via updating their interaction matrix at each time step. In this study, I used random matrix theory and Lotka-Volterra analysis according to May's initiated tradition to ensure that my results are comparable to the long list of studies that followed. However, this approach has faced a great deal of criticism. Firstly, species interaction strengths in empirically derived community matrices are not independent and identically distributed thus not ideal in predicting the stability of real ecosystems. Secondly, among the most severe assumptions, it considers a linear approximation of the dynamics in the neighbourhood of the equilibrium. However, due to constant disturbance, real ecosystems are rarely at steady state.

Since May's paper [1], a great stability-complexity debate ensued on complex communities' maintenance and list of mechanisms have been hypothesized as factors to resolve this paradox. My results yield new insights and novel proposition to this existing research. Results from the study demonstrate that adaptation mechanisms and spatial dynamics cannot be ignored if we want to get a much clearer view of what to expect in a time like this.

5.2 Synthesis

The objectives of this thesis were to: (i) incorporate elimination and optimization switching into a modified Lotka-Volterra model in simulating the competitive species dynamics in a single and metacommunity; (ii) revisit on complexity-stability paradox by checking the influence of species interaction switching with more focus on the influence of σ on interspecific competition strength; (iii) derive a new complexity-stability measure incorporating switching into May's stability criterion. These objectives I achieved as follows.

Firstly, I developed a modified Lotka-Volterra model by dividing the interaction strength into interaction coefficient and strength to enable species switching simulation. In this initial stage I focused my analysis only on a single community. Secondly, I carried out simulations from the model based on different values of connectance, species richness and competition strength while taking into account the two forms of switching (elimination switching and optimization switching). The results from my simulations showed that species interaction switching improves stability, productivity, evenness under low connectance, competition strength, and species richness. Thirdly, I developed a new stability criterion taking into consideration the switching influence on the May's stability criterion since switching showed a reduced destabilizing effect by extending the stability threshold. Lastly, switching-dispersal combination showed a new paradigm shift in view towards the complexity-stability debate. From my results switching-dispersal combination showed an improved community stability and productivity bringing out new perspective into the complexity-stability conundrum.

In future, I suggest using a heterogeneous community to validate the influence on the stability-complexity dilemma. Previous studies have shown that species and community heterogeneity have positive influence on the species coexistence in a community hence possibly influence on the stability-complexity debate.

Appendix A

Appendix

A.1 Code

All fuctions used in this work are available on my github account. You can access via the link https://github.com/LangatGilbert/MastersThesis

A.2 Supplementary information

In Chapter 3 Fig 3.2 we have plots for averaged data points for 50 networks each with combined community size of $20, 50, 100$ species. We here present one network view of how each network's productivity, rank abundance stability, and nestedness behaves.

Note 1: Relationship between network complexity, architecture, and stability

Community stability

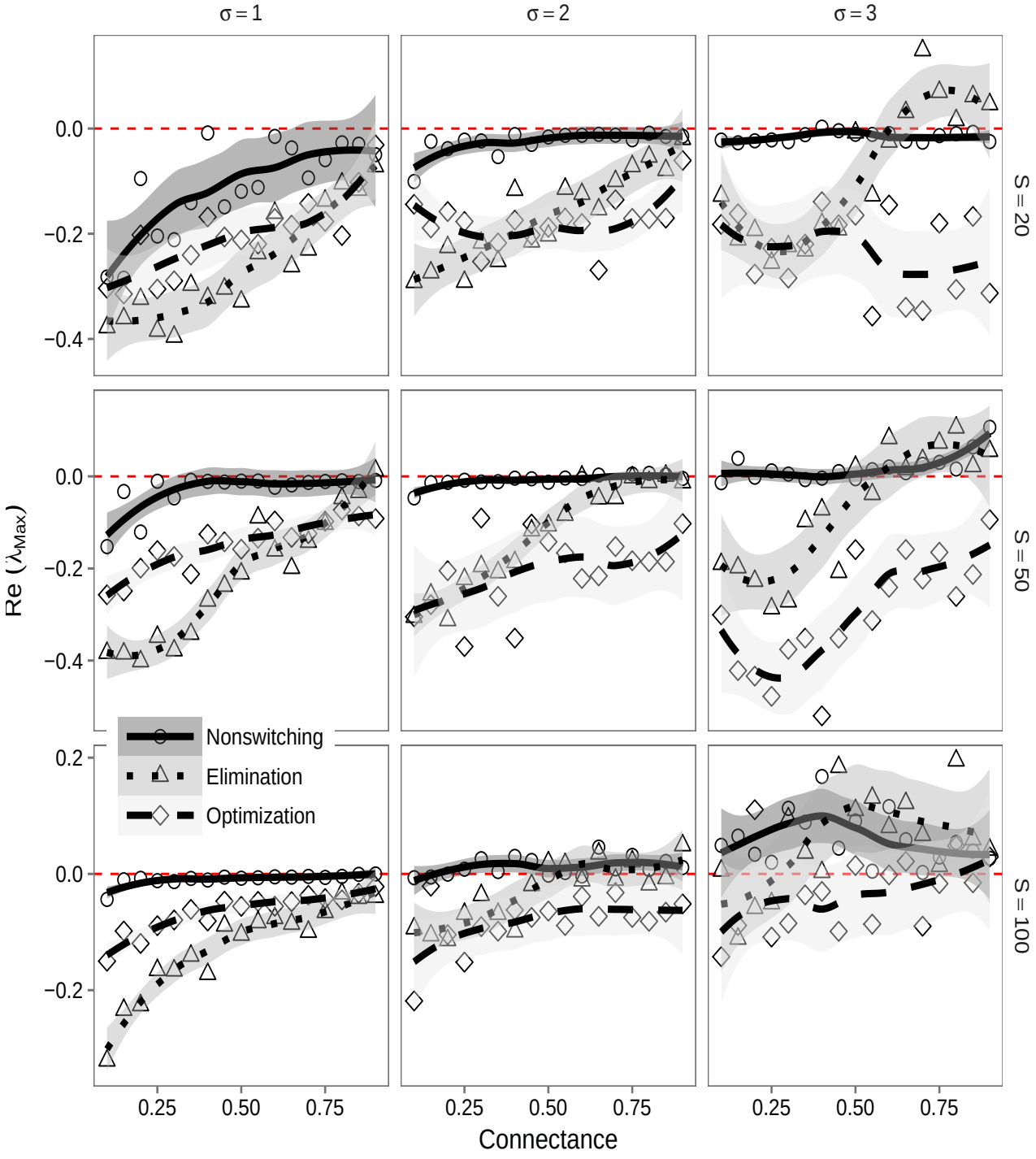


Figure A.1: **Relationship between network complexity and stability.** Stability denoted $\Re(\lambda_{Max})$ versus connectance with species population $S \in \{20, 50, 100\}$ (along the rows) and $\sigma \in \{0.1, 0.3, 0.5\}$ (along the columns). Regression curves were obtained using LOESS. System highly stable at low connectance, low σ and in simple structures $S = 20$. Switching improves stability.

To emphasize on the influence of the connectance and competition strength on stability we have plotted the eigenvalues distributions for various values of *Connectance* and σ as shown in Fig. A.2 and Fig. A.3 respectively.

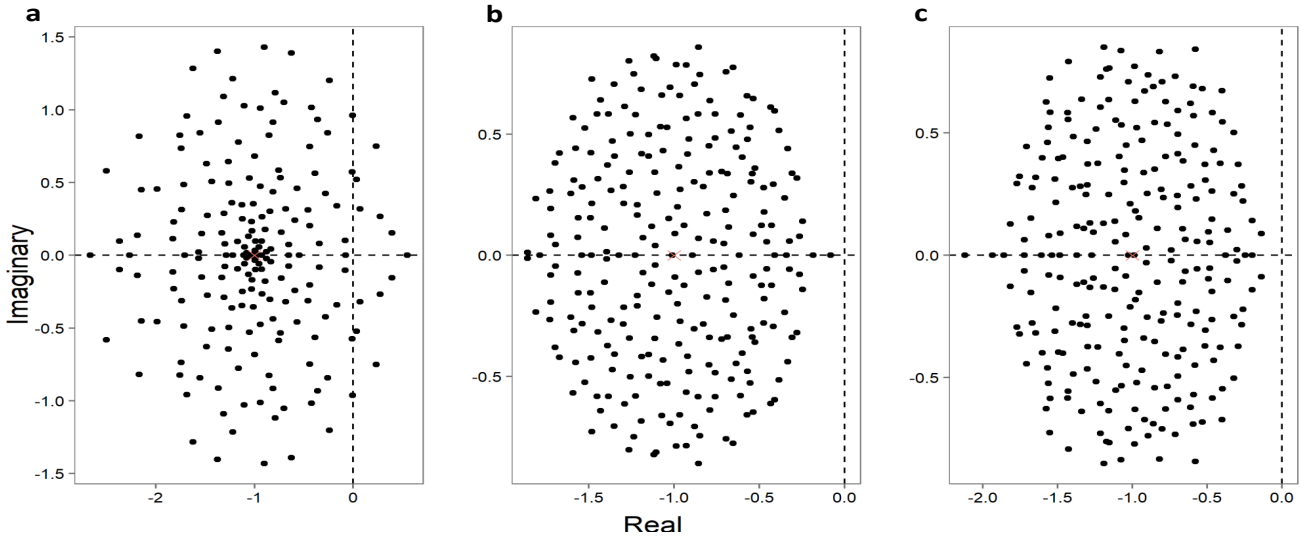


Figure A.2: **Illustration on the distribution of eigenvalues in a complex plane for different** *connectance* **values.** Distribution of the eigenvalues of community matrix **M** in the complex plane when $\sigma = 0.1$, $S = 250$, $m = 1$, $C = 0.1$, for **(a)** Non-switching, **(b)** Elimination, and **(c)** Optimization. Red stars indicate the centres of the eigenvalue distribution. This justifies on switching influence on stability. At **a** $\Re(\lambda_{Max})$ is positive implying instability while **b** and **c** the $\Re(\lambda_{Max})$ is negative hence both $\Re(\lambda_{Max})$ are stable.

To further illustrate the competition strength effect on the community stability, we also plotted the eigenvalues distribution on the complex plane for various values of σ. From Fig. A.1, low community strength implies better community stability.

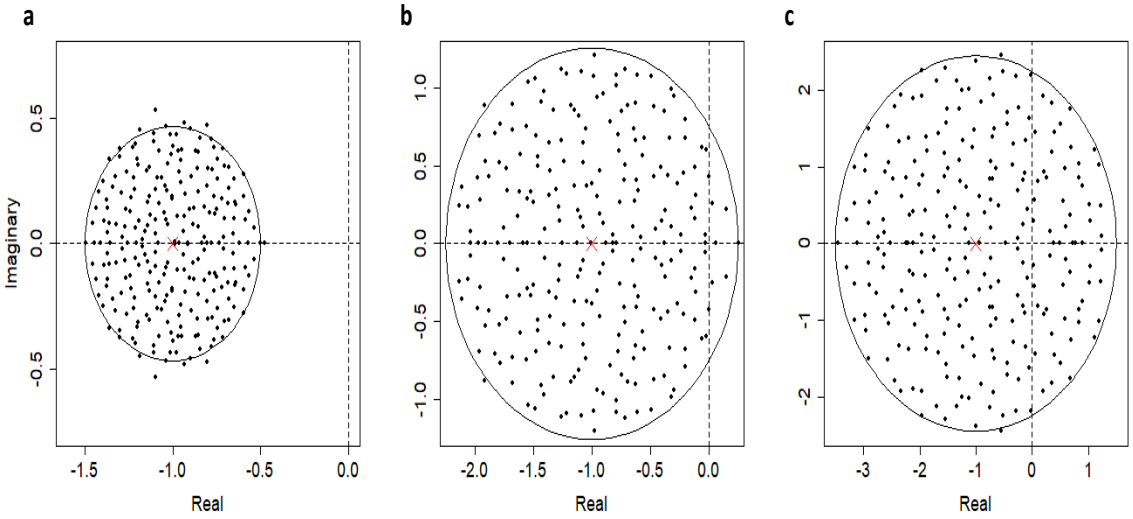


Figure A.3: **Illustrating σ influence on eigenvalues distribution.** Distribution of eigenvalues of the community matrix **M** when $S = 250, C = 0.1$ and **(a)** $\sigma = 0.05$, **(b)** $\sigma = 0.1$ **(c)** $\sigma = 0.2$. The red stars is the centres of the eigenvalues. At low species competition strength (**a**), all eigenvalues are on the left side of the complex plane illustrating a stable community while as the strength increases the community shifts instability.

Community Productivity

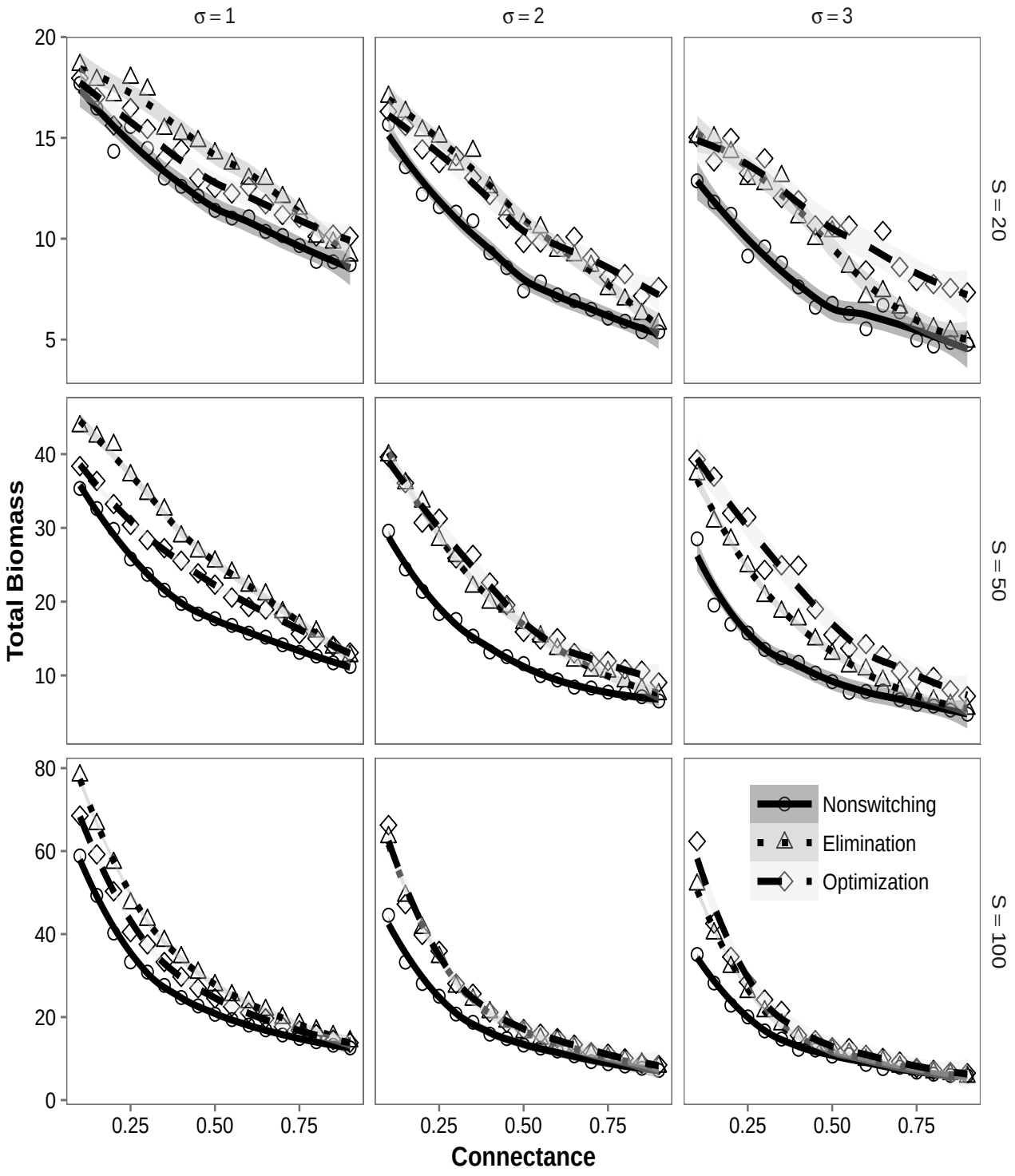


Figure A.4: **Effect of connectance on community productivity.** Productivity versus connectance with species population $S \in \{20, 50, 100\}$ (along the rows) and $\sigma \in \{0.1, 0.3, 0.5\}$ (along the columns). Regression curves were obtained using LOESS. Productivity is high at low connectance and low community strength σ with a negative correlation between productivity and connectance.

Rank abundance

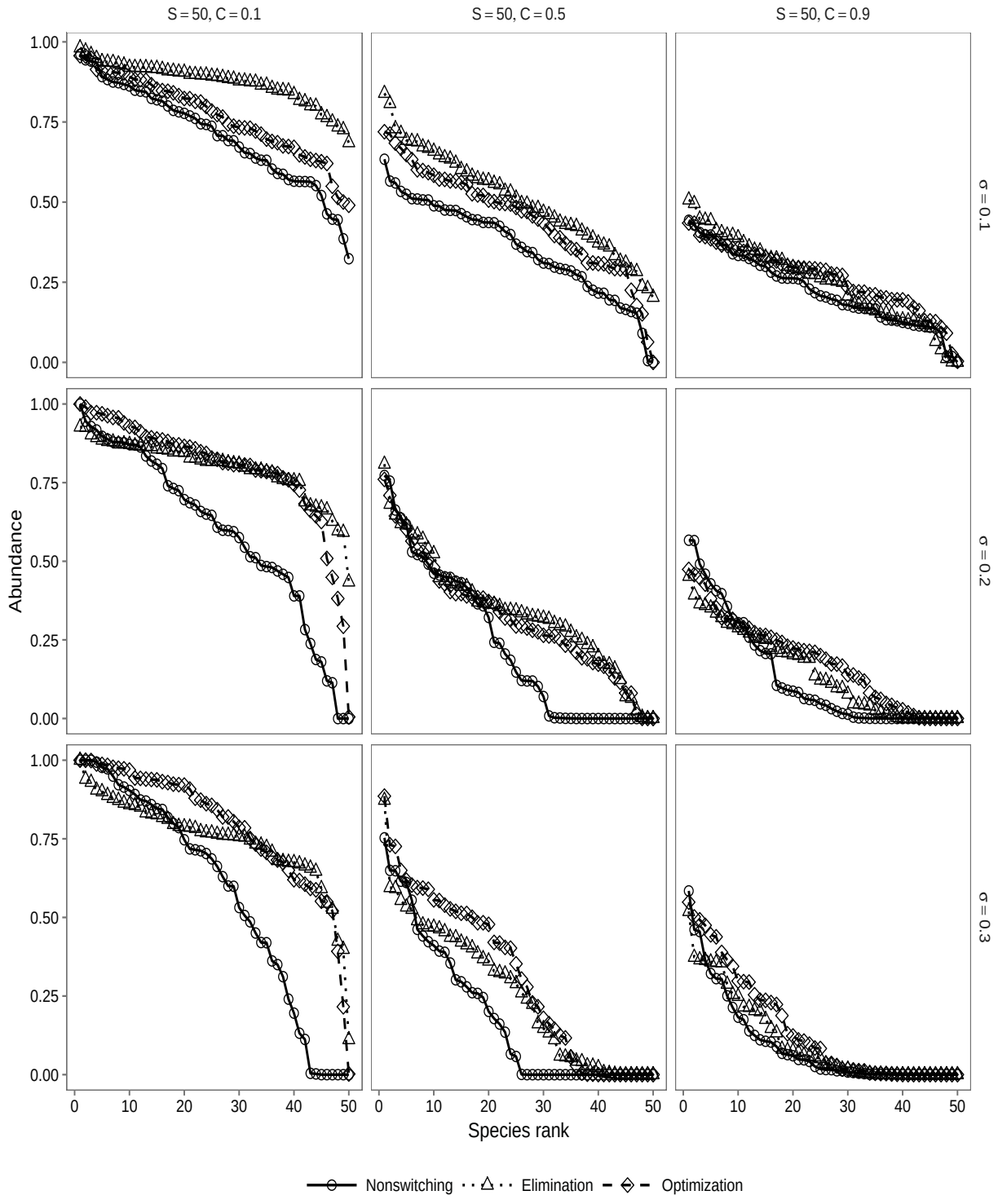


Figure A.5: **Species rank abundance curves for selected connectance values in a community of 100 species.** The plots visualizes a comparison between low $C = 0.1$ $(1^{st} column)$, moderate $C = 0.5$ $(2^{nd} column)$ and highly $C = 0.9$ $(3^{rd} column)$ connected communities. Influence of competition strength σ is reflected along the row plots from low to moderate competition strengths

Nestedness

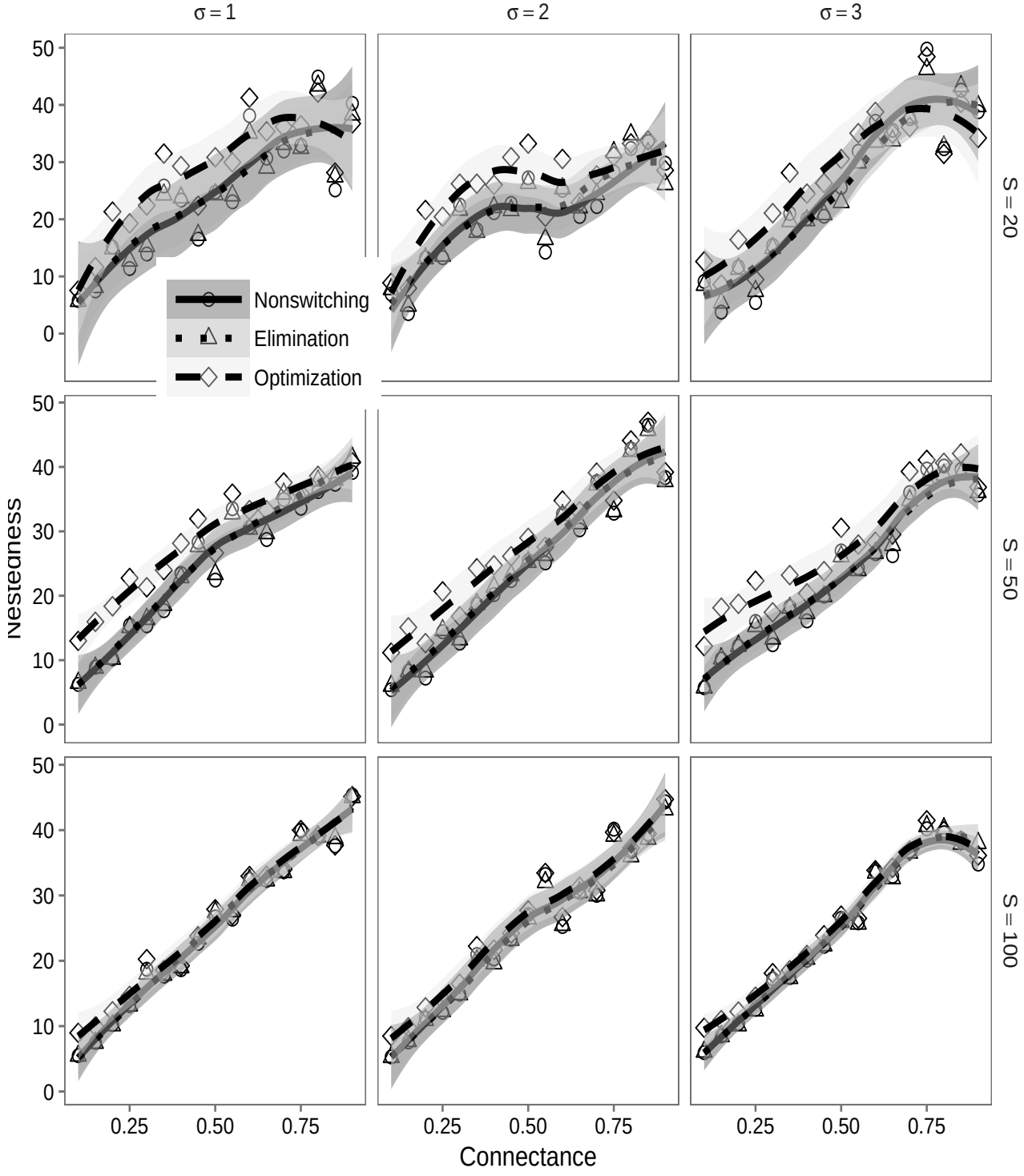


Figure A.6: **Nestedness-complexity relationship.** Computed in community with $S \in \{20, 50, 100\}$ and $\sigma \in \{0.1, 0.3, 0.5\}$. Regression curves were obtained using LOESS. Communities where optimization switching is practised are highly nested while elimination switching does not adversely influence nestedness.

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